Spatial conservation prioritization for Finnish forest conservation management

JOONA LEHTOMÄKI

LUOVA
Finnish School of Wildlife Biology, Conservation and Management

Department of Biosciences
Faculty of Biological and Environmental Sciences
University of Helsinki

ACADEMIC DISSERTATION

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SUPERVISED BY: Prof. Atte Moilanen
Department of Biosciences, University of Helsinki, Finland

REVIEWED BY: Dr. Panu Halme
Department of Biological and Environmental Science,
University of Jyväskylä, Finland

Dr. Niina Käyhkö
Department of Geography and Geology, University of Turku, Finland

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Section for Environment and Natural Resources,
University of Copenhagen, Denmark

CUSTOS: Prof. Atte Moilanen
Department of Biosciences, University of Helsinki, Finland

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Dr. Timo Kuuluvainen
Department of Forest Sciences, University of Helsinki, Finland

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"[...] one has to realize that 'society' is fundamentally divided. The utopian view held implicitly by many, that we 'are all in it together' and thus ought, as it were, to act in unison, is an illusion. There is no unity of aims, no close coincidence of interests, no consensus on responsibility, and there is no such thing as action that would be literally 'collective action' if that were to mean that we all act together. What we do have is a set of partial, contradictory concepts and tools for organized joint action."

Mermet et al. (2013)

CONTENTS

The thesis constitutes of the following articles, which the text refers to by their Roman numerals:

I **Lehtomäki J.**, Tomppo E., Kuokkanen P., Hanski I. & Moilanen A. (2009): Applying spatial conservation prioritization software and high-resolution GIS data to a national-scale study in forest conservation. *Forest Ecology and Management*. 258(11): 2439–2449. http://dx.doi.org/10.1016/j.foreco.2009.08.026

II Arponen A., **Lehtomäki J.,** Leppänen J., Tomppo E. & Moilanen A. (2012): Effects of connectivity and spatial resolution of analyses on conservation prioritization across large extents. *Conservation Biology*. 26(2): 294–304. http://dx.doi.org/10.1111/j.1523-1739.2011.01814.x

III Sirkiä S., **Lehtomäki J.,** Lindén H., Tomppo E. & Moilanen A. (2012): Defining spatial priorities for capercaillie Tetrao urogallus lekking landscape conservation in south-central Finland. *Wildlife Biology.* 18(4): 337–353. http://dx.doi.org/10.2981/11-073

IV **Lehtomäki J**., Tuominen S., Toivonen T., & Leinonen A. What data to use for forest conservation planning? A comparison of coarse open and detailed proprietary forest inventory data in Finland. *Manuscript*

V **Lehtomäki J.** & Moilanen A. (2013): Methods and workflow for spatial conservation prioritization using Zonation. *Environmental Modelling and Software*. 47: 128–137. http://dx.doi.org/10.1016/j.envsoft.2013.05.001

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AA: Anni Arponen
AL: Antti Leinonen
AM: Atte Moilanen
ET: Erkki Tomppo
IH: Ilkka Hanski
HL: Harto Lindén
JL: Joona Lehtomäki
JLep: Jarno Leppänen
PK: Panu Kuokkanen
SS: Saija Sirkiä
ST: Sakari Tuominen
TT: Tuuli Toivonen

ABBREVIATIONS

Abbreviation	Full term	Details	Explained in
ABF	Additive Benefit Function	Cell-removal rule in Zonation	3.5.1
CAZ	Core Area Zonation	Cell-removal rule in Zonation	3.5.1
DS	Distribution smoothing	Connectivity method in Zonation	3.5.2
IA	Interaction connectivity	Connectivity method in Zonation	3.5.2
LSI	Landscape identification	Post-processing feature in Zonation	4.6
MC	Matrix Connectivity	Connectivity method in Zonation	3.5.2
MetZo	Zonation Decision-support for METSO	Applied project	3.2
MS-NFI	Multi-source National Forest Inventory	Data source	3.3.1
NFI	National Forest Inventory	Data source	3.3.1
PriFRI	Private Forest Resource Inventory	Data source	3.3.1
PubFRI	Public Forest Resource Inventory	Data source	3.3.1

ORGANIZATIONS

Abbreviation	Organization	Role
ELY	Centre for Economic Development, Transport, and the Environment	Responsible for the regional implementation and development tasks of the central government. 15 centres in 2014.
FFC	Finnish Forest Centre	A state-funded organization tasked with promoting forestry and related livelihoods, advising landowners on forest management, collecting and sharing data related to Finland's forests and enforcing forestry legislation.
FGFRI	Finnish Game and Fisheries Research	A governmental, sectoral research institute, subordinate to the Ministry of Agriculture and Forestry.
JyU	University of Jyväskylä	Research university.
MAF	Ministry of Agriculture and Forestry	Steers the policy on sustainable use of natural resources. Legislative work is carried out as part of the Finnish Government and the EU institutions and decision-making.
ME	Ministry of Environment	Responsible for preparing matters to be submitted for consideration by the Government and Parliament, matters concerning communities, the built environment, housing, biodiversity, sustainable use of natural resources and environmental protection.
Metla	Finnish Forest Research Institute	A governmental, sectoral research institute, subordinate to the Ministry of Agriculture and Forestry.
Metsähallitus FOR	Metsähallitus Forestry	Sales and marketing of wood to the forest industry and management of state-owned commercial forests.
Metsähallitus NHS	Metsähallitus Natural Heritage Services	Management of national parks and other conservation, wilderness, and hiking areas; protection of species and habitats; provision of hiking, hunting, and fishing services.
SYKE	Finnish Environment Institute	Both a research institute, and a centre for environmental expertise. Part of Finland's national environmental administration, and mainly operates under the auspices of the Ministry of the Environment.
Tapio	Tapio Consulting Services	Private consultant company that provides solutions for efficient and sustainable forest management and bioeconomy. Tapio provides services both for public and private sector.
UH	University of Helsinki	Research university.
URC	Uusimaa Regional Council	A joint regional authority for Helsinki-Uusimaa Region. Tasks include regional and land-use planning and the promotion of local and regional interests in general.

ABSTRACT

In a world of competing interests and increasing land use pressures, the allocation of limited resources for biodiversity conservation need to be prioritized. Spatial conservation prioritization deals with the cost-efficient and well-balanced identification of priority areas for biodiversity, as well as with the allocation and scheduling of alternative conservation actions.

Finland is the most forested country in Europe, but more than 90% of Finland's forests are under commercial management. A history of widespread and relatively intensive forest management has led to many specialist species and habitats becoming threatened. At the same time, the protected area network is unequally distributed over the country, with largest areas in the north where species diversity is lowest. Consequently, the current main priority for conservation action for forest habitats is expanding the protected area network in the southern parts of the country in an ecologically justified way.

In this thesis, I have three specific objectives. First, I examine the suitability of commonly available forest inventory data for informative high-resolution spatial conservation prioritization. Second, I clarify the effects of spatial scale and connectivity on spatial conservation prioritization at regional and national extents. Finally, I develop, demonstrate, and implement a practical workflow for regional- and national-scale forest conservation management planning in Finland, using the Zonation framework and software for spatial prioritization.

The thesis consists of a summary and five chapters. In Chapter **I** of this thesis, I introduce a novel approach in expanding the forest reserve network in Finland using forest inventory data, expert knowledge, and Zonation. In Chapter **II**, I turn to the effects that data resolution and connectivity have on conservation prioritization results. Chapter **III** introduces a focal-species approach developed for the capercaillie (*Tetrao urogallus*). Chapter **IV** seeks to clarify the usefulness of open forest inventory data in conservation prioritization compared to more detailed proprietary data in Finland. Finally, in Chapter **V**, I collate and discuss the best practices in planning and executing a conservation prioritization project using the Zonation framework.

I show how habitat quality indices based on forest inventory data and expert knowledge can be used as a basis of conservation prioritization. Comparison against validation datasets reveals that the analyses do indeed produce informative priorities. Case studies involving the expansion of the national protected area network both on public and private land demonstrate how the results can be applied in the context of a national forest conservation program, METSO. The spatial resolution of input data should closely match those of the planning objectives and the ecological processes involved, as results based on coarse-resolution analyses can substantially deviate from high-resolution analyses. Furthermore, the level of detail in the forest inventory data defines how well the prioritization is able to identify small occurrences of important forest types and key habitats.

The quality and the quantity of suitable habitat between protected areas are important for many forest species. Accounting for connectivity in the prioritization analyses produces spatially more aggregated priority patterns. However, there is an inherent and almost inevitable trade-off between connectivity and local quality: emphasizing connectivity will lower the relative value of locally high quality, but poorly connected sites. Therefore, the balance between connectivity and local habitat quality merits careful consideration in spatial prioritization.

My thesis highlights important factors to consider in implementation-oriented spatial conservation prioritization. First, data availability often restricts the types of prioritization analyses that can be undertaken. Therefore, long-term development of high-quality open access data is crucial for making best use of spatial prioritization approaches. Second, establishing a conceptual model for the prioritization process can help formulate the right questions, to select the most suitable tools, and to estimate the costs and benefits involved. Finally, a successful conservation prioritization requires participation of experts and stakeholders. Methods, analyses, workflows and visualization techniques summarized in this thesis can serve as starting points for other similar applications elsewhere and support meeting local, regional and global conservation goals.

TIIVISTELMÄ

Kilpailevien intressien ja kasvavien maankäyttöpaineiden maailmassa luonnonsuojeluun kohdennettavat voimavarat tulee käyttää järkevästi. Spatiaalisessa suojelupriorisoinnissa pyritään luonnonsuojeluun sopivien alueiden kustannustehokkaaseen ja monipuoliseen tunnistamiseen, sekä vaihtoehtoisten suojelutoimenpiteiden ajalliseen ja alueelliseen kohdentamiseen.

Suomi on Euroopan metsäisin maa, mutta yli 90 prosenttia Suomen metsistä on talouskäytössä. Laajan ja verrattain voimaperäisen metsänkäyttöhistorian vuoksi monet suomalaiset metsälajit ja -elinympäristöt ovat uhanalaistuneet. Hankalaksi tilanteen tekee se, että Suomen suojelualueverkosto on epätasaisesti jakautunut: Suojeluaste on suurin pohjoisessa, vaikka siellä lajiston monimuotoisuus on matalinta. Tämän hetken kiireellisin suojelutoimenpide onkin suojelualueverkoston ekologisesti perusteltu laajentaminen Etelä-Suomessa.

Väitöskirjani keskittyy spatiaaliseen suojelupriorisointiin suomalaisessa metsäkontekstissa kolmen päätavoitteen kautta. Yhtäältä tarkastelen suomalaisten metsävaratietojen soveltuvuutta tarkan spatiaalisen priorisoinnin lähtöaineistoksi. Toiseksi tutkin millaisia vaikutuksia valitulla mittakaavalla ja kytkeytyvyydellä on spatiaalisen suojelupriorisoinnin tuloksiin alueellisella ja valtakunnallisella tasolla. Kolmanneksi pyrin osoittamaan, kuinka spatiaalista Zonation-ohjelmistoon nojaavaa suojelupriorisointia voidaan hyödyntää käytännön suojelusuunnittelutyössä.

Väitöskirjani koostuu johdannosta ja viidestä osatyöstä. Osatyössä **I** esittelen uuden tavan suojelualueverkoston laajentamiseen valtionmailla, hyödyntäen erityyppisiä metsävaratietoja, asiantuntijatyötä sekä Zonation-ohjelmistoa. Osatyössä **II** tarkastelen mittakaavan ja kytkevyyden merkitystä suojelupriorisoinnissa. Osatyössä **III** osoitan, kuinka spatiaalisen suojelupriorisoinnin menetelmiä voidaan soveltaa metson (*Tetrao urogallus*) soidinmaisemien paikallistamiseen. Osatyössä **IV** tutkin, kuinka hyvin avoimesti saatavilla olevaan metsävaratietoon pohjautuva suojelupriorisointi toimii suhteessa priorisointiin, joka perustuu tarkempaan, mutta suljettuun metsävaratietoon. Viimeisessä osatyössä **V** tunnistan ja kuvaan parhaita käytänteitä suojelupriorisointiprosessin läpiviemiseksi.

Työni tulokset osoittavat, että metsävaratietoon ja asiantuntijatyöhön pohjautuvat, suojeluarvoa kuvaavat indeksit voivat toimia informatiivisen suojelupriorisoinnin pohjana. Lisäksi osoitan tapaustutkimusten kautta, kuinka spatiaalisen suojelupriorisoinnin tuloksia voidaan soveltaa kansallisen suojeluohjelman, METSO:n, puitteissa sekä yksityisettä valtionmailla. Tällöin käytettävän aineiston resoluution tulee kuitenkin olla linjassa suojeluongelman sekä siihen liittyvien ekologisten prosessien mittakaavan kanssa. Karkean resoluution aineistoon pohjautuvat spatiaalisen suojelupriorisoinnin tulokset voivat poiketa huomattavasti tarkemman resoluution aineistolla tuotetuista tuloksista. Lisäksi aineiston yksityiskohtaisuus ja rakenne määrittävät pitkälti, kuinka hyvin analyysit pystyvät huomioimaan pienipiirteisiä metsäelinympäristöjä.

Suojelualueiden välillä sijaitsevien metsäalueiden määrä ja laatu ovat tärkeitä tekijöitä monien metsälajien kannalta. Ekologisen kytkeytyvyyden huomioiminen tuottaa alueellisesti keskittyneempiä suojeluprioriteetteja. Kytkeytyvyyden korostaminen alueellisesti saattaa kuitenkin laskea paikallisesti korkealaatuisten, mutta huonosti kytkeytyneiden alueiden suhteellista arvoa. Kytkeytyvyyden ja paikallisen laadun tasapainoinen huomioimien suojelupriorisoinnissa vaatii siten harkintaa.

Väitöskirjani tunnistaa toteutukseen tähtäävän suojelupriorisoinnin kriittisiä kohtia. Yhtäältä aineiston saatavuus on usein suojelupriorisointianalyysien laatua rajoittava tekijä. Siksi pitkäjänteinen ja avoimeen tietoon perustuva aineistopolitiikka on tarpeen. Toiseksi, priorisointiprosessin osana luotava käsitteellinen malli auttaa muotoilemaan päätöksentekoon liittyvät kysymykset oikein, valitsemaan tehtävään sopivat työkalut sekä arvioimaan työhön liittyvät kustannukset ja hyödyt. Kolmanneksi on tärkeää tunnistaa, että menestyksekäs suojelupriorisointi edellyttää laajaa asiantuntija- ja sidosryhmäyhteistyötä. Toivon, että väitöskirjassani esitetyt analyysit, työvuot ja visualisointitavat toimisivat pohjana muille vastaaville sovelluksille ja siten tukisivat paikallisten, alueellisten ja globaalien suojelutavoitteiden toteutumista Suomessa ja kansainvälisesti.

SUMMARY

Joona Lehtomäki

Metapopulation Research Group, Department of Biosciences, PO Box 65 (Viikinkaari 1), 00014 University of Helsinki, Finland

1 INTRODUCTION

Resources available for conservation are always limited and making well-balanced conservation decisions calls for sound scientific understanding of the underlying ecological, economic, and decision-theoretic concepts and phenomena. During the last 15 years, the field of systematic conservation planning has emerged as one of the leading paradigms in providing decision-support on conservation priorities and assisting effective implementation (Margules & Pressey 2000; Pressey & Bottrill 2009; Knight et al. 2010; Kukkala & Moilanen 2012). Within the broader context of systematic conservation planning, spatial conservation prioritization involves analytical activities tackling the questions of when, where, and how we should act to achieve conservation goals efficiently (Ferrier & Wintle 2009; Kukkala & Moilanen 2012). Spatial conservation prioritization forms the conceptual background for my work in this thesis. Despite the steep increase in the number of publications on spatial conservation prioritization (see Moilanen et al. (2009d) for illustration), crucial questions still remain to be answered. The conceptual and theoretical underpinnings of spatial conservation prioritization have been well established, but better understanding on how different types of data (e.g. Carvalho et al. 2010), scale of planning (e.g. Larsen & Rahbek 2005), and connectivity (e.g. Pascual-Hortal & Saura 2007) should be handled is needed and such knowledge would also have great practical utility. While many questions related to spatial conservation prioritization merit scientific investigation in their own right, I have always been strongly motivated by research that has clear connections to on-the-ground conservation implementation. The chapters of this thesis therefore deal with conceptual and methodological aspects of spatial conservation prioritization while always considering the implications of real-life implementation. In other words, the work has taken place at the interface of methodological spatial conservation prioritization and implementation-oriented conservation planning.

I have done all of the research presented in this thesis in the context of conservation management of Finnish forests. For this, I have several reasons.

First, Finnish forest biodiversity is becoming increasingly threatened. In spite of over two-thirds of the country being covered by forests, Finland has practically no natural forest left (Kuuluvainen & Aakala 2011) and more than 90% of forested land is under commercial forest management (Finnish Forest Research Institute 2013). In Finnish forests, habitat loss is not about deforestation, but rather about far progressed and extensive transformation of forests into production landscapes, which is visible in the number of threatened species and habitats: 36.2% of threatened species are primarily forest species (Rassi et al. 2010), and 70% forest habitats are considered threatened (Kontula & Raunio 2009).

Second, the forest reserve network of Finland is concentrated to the northern parts of the country with low levels of protection in the south where forests have relatively much higher species and habitat richness and diversity (Virkkala et al. 2000; Kuuluvainen 2009). Finding ecologically justified ways of expanding the reserve network in southern Finland is not only a scientifically interesting topic, but it also has real importance within Finnish environmental administration, as I will explain later in this thesis.

Third, databases and advanced decision-support systems developed for commercial forest management provide opportunities for spatial conservation prioritization. For many species and habitats, we do not have observational data over large extents. However, large quantities of forest inventory data potentially suitable for spatial conservation prioritization are available. If we can integrate spatial conservation prioritization methods with existing forest planning information systems and data, they would be immediately applicable over large extents of commercially managed forest landscapes. This point is important: because protected areas alone cannot stop the declining biodiversity trends, conservation actions must also be targeted to areas between protected areas (Hanski 2011).

Fourth, and finally, most of Finnish forests are part of the circumpolar boreal forest zone that is facing similar kinds of anthropogenic threats in many other countries. The research I present in this thesis is partly specific to Finland, but the general conclusions, the methodology, and workflows can be adapted and applied in other regions and countries that have similar kinds of spatial conservation planning needs.

In this thesis, I set out to develop and implement an approach for quantitative spatial forest conservation prioritization in Finland. More specifically, my objective in this thesis is:

1. To understand the suitability of commonly available forest inventory data for informative high-resolution spatial conservation prioritization in Finnish forests.

2. To dissect the effects of scale and connectivity on spatial conservation prioritization at regional and national extents.

3. To develop, demonstrate, and implement a practical workflow for regional- and national-scale forest conservation management planning in Finland.

1.1 SPATIAL CONSERVATION PRIORITIZATION

Spatial conservation prioritization deals with the identification of priority areas for biodiversity, as well as the allocation and scheduling of alternative conservation actions to inform decision-making (Ferrier & Wintle 2009; Kukkala & Moilanen 2012). In other words, spatial conservation prioritization seeks to answer the question of where, when, and how we act to efficiently meet conservation goals (Wilson et al. 2007; Kukkala & Moilanen 2012). Efficiency is an important concept, as possible conservation actions are always limited by available resources, most notably money (Wilson et al. 2007, 2009b). Spatial conservation prioritization can be informative for many different types of conservation action (Pressey et al. 2007; Wilson et al. 2009a; see also Box 1).

Prioritizing between areas for new protected areas is the oldest and most common type of conservation action in the conservation prioritization literature (Kremen et al. 2008; Jenkins & Joppa 2009; Proctor et al. 2011; Leroux & Rayfield 2013). In cases where species have become threatened or where there is very little of the original habitats left, establishing protected areas is a priority in itself (Brooks et al. 2006; Le Saout et al. 2013). If extensive habitat transformation has already happened, as is the case in Finland for example, prioritizing between potential areas for other conservation actions such as restoration (Halme et al. 2013) is necessary as well.

Spatial conservation prioritization can be used as a form of technical assessment employed within the broader context of conservation planning (Margules & Pressey 2000; Knight et al. 2006b, 2013; Margules & Sarkar 2007; Moilanen et al. 2009e; Pressey & Bottrill 2009). Conservation planning (*sensu* Knight et al. (2013)) can be described as a complete operational model that covers all the stages necessary for successful conservation action including assessment, planning, and management. Regardless of the planning framework which spatial conservation prioritization should inform, it is necessary that various high- and low-level objectives are defined explicitly and quantitatively at the outset of a planning process (Ferrier & Wintle 2009; Runge et al. 2011). High-level objectives define the desired

Box 1. What are the results of spatial conservation prioritization useful for in forest conservation? (Adapted from V)

1. **Identification of ecologically most and least important areas.**
   The most important areas are candidates for conservation actions such as establishing protected areas. The least important areas on the other hand are candidates for alternative land uses such as intensive forestry.
2. **Targeting of financial incentives for conservation.**
   How to allocate limited financial resources across different locations? Incentives could be e.g. financial compensations for landowners for protecting their forest.
3. **Evaluation of existing or proposed protected areas.**
   How effective and well balanced is the present or some proposed reserve network? Would some other configuration be more optimal?
4. **Targeting of habitat maintenance and restoration.**
   Improving the quality of forest habitats through habitat maintenance and restoration not only creates more suitable habitat but also increases the connectivity of the PA network.
5. **Target-based planning.**
   While setting independent targets for biodiversity features (e.g. "protect 17% of habitat *A* and 12% of habitat *B*") may lead to suboptimal solutions, in real-life situations conservation targets are often used because they are easy to understand and monitor.
6. **Climate change mitigation and adaptation.**
   If the anticipated effects of climate change can be modeled, then the effects can be incorporated into conservation prioritization as well. Results may be useful in maximizing the carbon storage potential of forests and in establishing new protected areas.
7. **Biodiversity offsetting.**
   If forest management operations, such as clear-cutting, cannot be avoided in a given location, then one should seek to compensate for the ecological loss by protecting (or stopping decline of) the same type of habitat somewhere else.

collective outcomes of conservation actions (and other land use decisions), and they are driven by societal, political, and cultural values (Ferrier & Wintle 2009). Slowing down or stopping the decline of forest biodiversity by a given year is an example – albeit a vaguely formulated one – of a high-level objective. Low-level objectives, such as quantifying the current state of forest biodiversity and assessing the likely impact of one potential action, are typically more technical in nature (Ferrier & Wintle 2009). Factors identified by the low-level objective directly feed into the spatial conservation prioritization process. However, setting clear high-level objectives and translating them into low-level objectives is generally not an easy task (Ferrier & Wintle 2009); failure in asking the right questions will prevent us from collating information on the relevant factors and ultimately from giving informative answers to support conservation decision-making.

All conservation prioritization is not necessarily quantitative (Ferrier & Wintle 2009), i.e. involving quantitative spatially explicit data and formal methods. Practitioners, managers, and various other stakeholders have intricate knowledge on the ecological and socio-political patterns and processes especially at the local scale. This knowledge can be used to prioritize between areas and conservation actions either directly (Hannah et al. 1998) or by combining expert-knowledge with computational information systems in participatory planning (Pert et al. 2013). Expert-based prioritization can be fast and relatively cheap to do, but it also has several disadvantages. Experts regularly have different cognitive biases, such as over-confidence in their own knowledge (Speirs-Bridge et al. 2010; Martin et al. 2012), which might consequently result in biased priorities. While experts might be well aware of the occurrence of species and habitats in their own region, they are usually less well equipped to deal with the properties of large landscapes, compound entities such as reserve networks, and the effects of complex ecological phenomena such as connectivity.

To address the issues of purely expert-driven prioritization, many quantitative approaches to spatial conservation prioritization have emerged over the last two decades (Moilanen et al. 2009e). More specifically, the term "quantitative" refers to prioritization based on quantitative and spatially explicit data that describes the extent and occurrence of biodiversity features (e.g. species and habitats, see 1.4) and other relevant information (e.g. costs and threats (Wilson et al. 2007)). A prioritization algorithm then does the actual prioritization by ordering the planning units used according to some explicit formulation and the results are usually presented in the form of maps that describe the spatial distribution of priorities over the area of interest (e.g. Ferrier & Wintle 2009; Moilanen et al. 2011b).

The mathematical formulations and algorithmic implementations of spatial prioritization have been widely studied (Possingham et al. 2001; Williams et al. 2005a; Sarkar et al. 2006; Moilanen et al. 2009c) and currently several software implementations of these algorithms exist such as Marxan (Possingham et al. 2000), C-Plan (Pressey et al. 2009), ConsNet (Ciarleglio et al. 2009), and Zonation (Moilanen et al. 2014). Most of the modern approaches have a particular feature in common: they are based on the concept of complementarity. While several definitions for complementarity exist (see Kukkala & Moilanen 2012 for a review), "complementarity" can be loosely defined as a property of a prioritization solution whereby sites work together efficiently in achieving conservation objectives (Wilson et al. 2009b). Furthermore, selection of sites is dependent on conservation actions chosen and the spatial relationships between other selected sites (Moilanen 2008b).

Connectivity is another central concept for spatial conservation that is often also included in policy recommendations for conservation action (Heller & Zavaleta 2008; Hodgson et al. 2009). From the population-ecological perspective, shorter distances between habitat patches tend to facilitate species' dispersal and hence enhance (meta-) population viability over time (Hanski 1998; Bowne & Bowers 2004; Moilanen 2005). However, the exact relationship between population viability and connectivity is specific to species and locality (Nicholson & Ovaskainen 2009). Accounting for connectivity in reserve network design can be ecologically justified (Williams et al. 2005a; Wilson et al. 2009b; Hodgson et al. 2010). While connectivity affects population dynamics, it is the area and quality of available habitat that actually defines the regional carrying capacity for a species (Hodgson et al. 2009; Moilanen 2012). The corollary is that area and quality of habitats, or more generally the occurrence levels of biodiversity features, is the primary factor in spatial conservation prioritization, but including connectivity can much enhance the prioritization. Accounting for connectivity in practice can be difficult for several reasons. First, defining and measuring connectivity is not a simple task (Kindlmann & Burel 2008; Kool et al. 2013). Rayfield et al. (2011) listed more than 60 different connectivity measures. Second, operationalizing the concept of connectivity in the context of spatial conservation planning is not straightforward mathematically or computationally (Williams et al. 2005a; Moilanen et al. 2009c). During the past decade, however, there has been active research around the inclusion of connectivity considerations into spatial planning (Moilanen et al. 2009c).

While quantitative approaches to spatial conservation prioritization have distinct advantages, expert-based and quantitative approaches are not mutually exclusive. Factors can only be included in spatial prioritization if spatially explicit data describing their occurrence is available (see 1.4).

Unfortunately, detailed spatial data across large extents are usually not readily available and often we must rely on expert-opinion instead. Thus, expert-based and quantitative approaches complement each other in many ways (Ferrier & Wintle 2009).

1.2 FOREST MANAGEMENT AND BIODIVERSITY IN FINLAND

According to the latest Red List of Finnish species, 36.2% of threatened species are primarily forest species, and changes in the forest environment are the primary cause of threat for almost a third (30.8%) of all threatened species (Rassi et al. 2010). More specifically, the major causes of threat are a decrease in the amount of decaying wood and large trees, changes in the tree species composition and age structure of forests, and reduction of old-growth forest area (Rassi et al. 2010). Additionally, intensive forest management has altered and largely suppressed natural forest disturbance regimes that have created habitat heterogeneity and resources such as dead wood especially on fine scales (Kuuluvainen & Aakala 2011). These adverse effects on Finnish forest biodiversity have been brought about by the intensive forest management that started soon after the Second World War in 1940s (Esseen et al. 1997; Siitonen 2001; Kuuluvainen 2009). In its current form, the primary aim of Finnish forest management is securing the timber supply for the large and nationally important forest industry (Halme et al. 2013). The predominant management regime is based on a sequence of pre-commercial and commercial thinning followed by a clear-cut harvesting with a rotation time varying between 40 and 120 years (Kuuluvainen et al. 2012; Halme et al. 2013). While native tree species are favored, the current management bears in some areas resemblance to plantation forestry because of even-aged stand structure and the absence of natural variation in tree species composition and stand structure (Kuuluvainen 2009; Halme et al. 2013).

The need to reduce the adverse effects of intensive forest management through policy and planning has long been recognized in Finland (Haila 1994). Traditionally, the Finnish forest conservation policy has been based on public and private protected areas (Horne 2006). Nationally, 9% of forests (including forest land and poorly productive forest land) are strictly protected – this is the highest number of all of Europe. However, 87% of the protected forest area is in Northern Finland (Finnish Forest Research Institute 2013). In Southern Finland, the fraction of strictly protected forests is 2.3%. The figures are even lower if we only look at forests on productive land. Consequently, the most significant deficiency in the Finnish forest reserve network is the low level of protection in hemiboreal and southern and middle-boreal forest vegetation zones (Virkkala et al. 2000; Virkkala & Rajasärkkä 2006). The fraction of protected forests is especially low in Southern Finland where species persistence cannot be guaranteed in the long run unless the management of areas in between protected areas is improved (Rayfield et al. 2007; Timonen et al. 2011; Hanski 2011).

Sustainable forest management has had a prominent place in Finnish forest policies (Primmer & Kyllönen 2006; Vierikko et al. 2008). Since the 1990s, the shift towards more sustainable forest management has been partly driven by influences of international forest policy processes related to biodiversity conservation (Primmer & Kyllönen 2006; Lindstad & Solberg 2012). Another important driver is the changes in values of the forest industry mostly in response to growing market demand of sustainable forestry products (Kotilainen & Rytteri 2011). In Finland, conservation-oriented measures in forest planning and management include prolonged rotation times (Koskela et al. 2007), green-tree retention (Gustafsson et al. 2010), setting aside small biological hotspots called woodland key-habitats (Timonen et al. 2010, 2011), and forest certification (Parviainen & Frank 2003; Koskela et al. 2007). While some of these measures are voluntary, others are required by law. For example, forest certification is voluntary, but leaving areas defined as woodland key-habitats outside forestry operations is mandatory. Measures have undoubtedly had positive effects, at least in slowing species declines, but the effectiveness of integrating these biodiversity conservation measures and production forestry is not conclusive (Parviainen & Frank 2003; Timonen et al. 2011; Runnel et al. 2013; Fedrowitz et al. 2014). In any case, these measures have not been successful in reversing the overall negative trend of forest biodiversity becoming more threatened (Rassi et al. 2010). Their effectiveness could arguably be enhanced if the implementation of these measures would be based on spatial conservation planning that would consider the complementarity and connectivity of candidate sites to the existing reserve network.

In Finland, the largest ownership category on forestry land is private forest owners (52%), followed by the state (35%), and companies (8%). In southern Finland, private forest owners have an even larger share (73%) and companies own more forestry land (12%) than the state (9%) (Finnish Forest Research Institute 2013). The number of private forest owners is very high too: At the end of 2011, 12% of the total population had forest property equal or greater than 2 hectares (Finnish Forest Research Institute 2013). The average size of a forest property is ca. 30 ha, which is quite small in international comparison. In summary, forest ownership and land-tenure is highly fragmented especially in Southern Finland, setting some constrains on forest management and conservation planning.

More recently, forest-owners have had the possibility to participate in government- funded conservation programmes, most notably the METSO-programme, which is based on voluntary action

Box 2. The Forest Biodiversity Programme METSO 2008–2025

METSO is a Finnish government funded conservation programme that aims at halting the ongoing decline of habitats and species, and at establishing stable favorable trends in South Finland's forest ecosystems. The Ministry of Environment and the Ministry of Agriculture and Forestry collaborate in implementing the programme that covers both state-owned and private forests. The original government resolution (Finnish Government 2008) set objectives of establishing 96 000 ha of new protected areas on private land and 10 000 ha on state-owned land. Protected areas on private land can be either permanent or temporary 10-year contracts. In addition to establishing new protected areas, METSO also targets at employing nature management and preservation of valuable forest biotopes in ~100 000 ha of commercially managed forest. Authorities responsible for the implementation of METSO on private land are the Centres for Economic Development, Transport, and the Environment (ELY Centres) and the Finnish Forest Centre (FFC). On state-owned land, Metsähallitus (the Finnish Forest and Park Service) is responsible for METSO-implementation. For the spatial extent of METSO, see Figure 2.

METSO is based completely on voluntariness. Authorities evaluate forest areas offered by forest-owners based on a set of ecological selection criteria and if the offered forest area fulfills these criteria, it is admitted into either permanent or temporary protection. A full financial compensation is paid to the forest-owner for the protection. The annual budget in 2014 was ~40 million €, out of which most is spent in compensation costs.

Since the selection of suitable sites depends on what the forest-owners offer, centralized planning of the reserve network is challenging. However, in many parts of the country the budget is not enough to compensate for all the offers that the authorities receive and they need to prioritize between the different offers. During 2010-2014, the Ministry of Environment has funded a cross-sectorial researcgh and development project (see 3.2) that has developed an approach based on the Zonation framework for prioritization in METSO.

By June 2014, METSO-programme had led to the conservation of ~30 000 ha of private forest and ~10 000 of state-owned forest. In the same month, the Finnish government revised the resolution on METSO (Finnish Government 2014) extending the METSO period to 2025 and refining some of the objectives such as mandating an additional 13 000 ha to be protected on state-owned land. Chapter **I** in this thesis deals with prioritizing between suitable sites for METSO in state-owned forests and Chapter **IV** is related to METSO prioritization that has been done in private forests.

(Finnish Government 2008; Juutinen et al. 2009; Primmer et al. 2013; see also Box 2). Voluntary agreements (Mäntymaa et al. 2009) are a particular type of policy-instrument by which private forest-owners are financially compensated for nature conservation on their land. Research into the cost-efficiency of voluntary agreements has had mixed results and efficiency typically depends on many factors, but socially voluntary agreements are often considered more acceptable by forest-owners than more conventional mandatory approaches (Wätzold & Schwerdtner 2005; Horne 2006; Mäntymaa et al. 2009; Mönkkönen et al. 2009). Voluntary forest conservation does pose particular planning and prioritization problems. The pool of potential sites for conservation is restricted to what forest owners voluntarily choose to offer. Hence, it is hard to anticipate the area, the quality, and the location of sites that become available.

1.3 SPATIAL PLANNING AND CONSERVATION MANAGEMENT IN FORESTS

Modern forest management planning is typically multi-objective taking into account economic, ecological, and social aspects simultaneously (Store & Kangas 2001; Bettinger & Sessions 2003; Kangas et al. 2008; Kotilainen & Rytteri 2011; Bradford & D'Amato 2012). Information systems that support decision-making on strategic, tactical, and operational levels of forest management are numerous and widely deployed. Many forest management activities, such as scheduling and targeting of harvesting have a strong spatial component, and thus spatially explicit forest management planning has been attracting increasing interest both academically and in practice (Bettinger & Sessions 2003; Baskent & Keles 2005). Spatial forest management also routinely translates plans across different spatiotemporal levels of planning: strategic planning, which takes place over large areas and long time-periods, feeds into more mid-term and often regional level tactical planning, which in turn is translated into local-level operational actions (Church et al. 2000). SCP and spatial conservation prioritization are also regional level activities, as are many of their key concepts such as complementarity and connectivity, which are spatiotemporal attributes of collections of sites, not individual sites (Wilson et al. 2009b).

From these broad definitions, it is clear that the objectives of spatial forest management overlap with those of spatial conservation prioritization, albeit the theoretical underpinnings of the two are different. In fact, Ferrier and Wintle (2009) note that "Spatial conservation prioritization is potentially applicable to any planning activity involving spatial choice in the location of actions affecting conservation outcomes". The full potential of quantitative spatial conservation prioritization can only be realized with effective mainstreaming and linking of conservation planning principles, techniques, and outcomes to other disciplines such as land-use planning and natural resource management (Pierce et al. 2005; Knight et al. 2006a; Ferrier & Wintle 2009). This is especially important on private land and at the local scale, where a large number of individual forest owners are driven by myriad personal motivations (Paloniemi & Tikka 2008). Most private forest owners depend on forestry professionals in planning and implementing both forest and conservation management (Hujala et al. 2007; Primmer 2011; Similä et al. 2014). Therefore, professional organizations and service providers have a central role in all types of management planning in private forests – including conservation management. A single organization, Metsähallitus (the Finnish Forest and Park service), governs and manages all state-owned forests. In state-owned forests, there are conceivably better prospects for top-down type of planning, whereas on private land dealing with a large number of forest owners implies a need for more distributed and bottom-up type of planning.

Broadly speaking, most of the studies that concern spatial forest conservation management in Finland belong to one of the two following categories: harvest scheduling or reserve network design (Kurttila 2001; Bettinger et al. 2003; Williams et al. 2005b; Marshalek et al. 2014). Spatial harvest scheduling means the spatiotemporal planning of harvest treatments in a way that satisfies given objectives, such as revenue maximization subjective to various economic and ecological constraints (St. John & Tóth 2013). For example, Kurttila and Pukkala (2003) used MONSU software (Pukkala 2004) to present a hierarchical spatial planning scheme that incorporated forest-owner-specific goals on timber production, while clustering the breeding and foraging areas for the flying squirrel (*Pteromys volans*). Jumppanen et al. (2003) also used MONSU to develop a practical harvest scheduling approach. Their approach clustered the occurrence of old-growth forests, while simultaneously satisfying given timber production goals. Mönkkönen et al. (2011) studied the spatiotemporal cost-efficiency of various conservation management regimes in Central Finland by combining forest stand simulator MOTTI (Salminen & Hynynen 2001) with spatially explicit landscape event simulator SELES (Fall & Fall 2001). They also assessed tradeoffs between conservation benefits and losses in timber harvest produced by different conservation management regimes. Later, Mönkkönen et al. (2014) used a similar approach, but this time looking for the landscape level optimal combination of management alternatives using multi-objective optimization.

Reserve design approaches are driven by ecological rules and computational methods to select optimal or near-optimal sets of forest reserves (Williams et al. 2004; Marshalek et al. 2014). The two alternative optimization approaches used to solve reserve design problems are exact optimization methods, such as integer programming (Sarkar et al. 2006; Haight & Snyder 2009), and heuristic methods (Moilanen & Ball 2009). Exact optimization methods can find a guaranteed globally optimal solution for the planning problem. However, application of exact optimization may imply simplifying assumptions that often do not correspond to the complex nature of real-world conservation problems. Furthermore, as the number of optimization objectives gets larger (e.g. when objectives include spatial considerations) and when the number of planning units (such as forest stands) increases, computation quickly becomes intractable (Sarkar et al. 2006; Kangas et al. 2008; Moilanen 2008a). Heuristic methods do not guarantee an optimal solution, but seek for good enough (i.e. near-optimal) solutions (Kangas et al. 2008; Moilanen & Ball 2009). In exchange for a potentially sub-optimal solution, heuristic methods are able to cope with more complex problems and problem sizes far greater than exact optimization methods. These methods have also been used to study optimal reserve design in Finnish forests. For example, Siitonen et al. (2002) developed a multi-objective greedy heuristic method to select a set of old-forest sites that best complement the existing reserve network while minimizing the costs. Juutinen et al. (2008) used the multi-source National Forest Inventory data (see 3.3.1) to build a habitat quality index, which they in turn used in a heuristic site selection model to maximize biological benefits under a given budget constraint. Kallio et al. (2008) used similar indices based on the same data in a spatial partial equilibrium modeling approach that simulated the Finnish forest sector for optimal regional allocation of sites for forest conservation. In this thesis, I make extensive use of a particular heuristic framework for spatial conservation prioritization, Zonation (**I**-**V,** 3.5).

1.4 DATA REQUIREMENTS AND ECOLOGICAL MODELS OF CONSERVATION VALUE

The data requirements of spatial conservation prioritization can be substantial. The types and amounts of data needed depend on the specific decision need and on the methods used, but main underlying data must be spatial, i.e. we must be able the map the particular data attributes to particular locations (Ferrier & Wintle 2009). Data describing the occurrence of different biodiversity features are in the core of any spatial conservation planning, because biodiversity is best protected where it occurs (Ranius & Kindvall 2006; Moilanen 2012). Most typically, biodiversity features are species (Leathwick et al. 2008; Rayfield et al. 2009; Meller et al. 2014), communities (Arponen et al. 2008; Moilanen et al. 2011b), habitat types (Klein et al. 2009; Kareksela et al. 2013), and ecosystem services (Moilanen et al. 2011a). Other types of data that are often relevant are data on costs (Pressey et al. 2007), current and future threats (Wilson et al. 2005), and the condition of habitats and ecosystems (Moilanen et al. 2011b). Moilanen (2012) provides a useful classification of different data types and their utility in spatial conservation planning. Relevant biodiversity features are mandatory for a biologically informative analysis; the need for other types of data depends on the planning objectives.

The spatial extent and objectives of planning define the resolution at which all data needs to be available.

On the other hand, the patterns of biodiversity we perceive through the data are influenced by the spatial extent and resolution of the observations underlying the data (Stoms 1994; Stohlgren et al. 1997; Rahbek 2005). Consequently, data resolution affects the outcome of conservation prioritization (Stoms 1992). The exact form and magnitude of this effect has remained largely unknown. Computational limitations often restrict our capability of using high-resolution data even when it exists; therefore, spatial aggregation of data sometimes cannot be avoided. However, using too coarse data may result in poor prioritization results biologically (Lombard et al. 1999) and economically (Richardson et al. 2006). In addition, the resolution of data should correspond to the planning units used in on-the-ground planning. The planning units used in spatial forest planning are typically forest stands, which implies that conservation prioritization should be done at a fine spatial resolution. Furthermore, planning for well-connected reserve networks requires that we can define the scale or scales over which connectivity is important for given biodiversity features (Beier et al. 2011).

An ecologically based model of conservation value is a conceptual construct that forms the foundation of spatial conservation prioritization (**V**, see also Figure 4). Here, the ecological model includes all spatial input data (and thus also the extent and resolution of the data), weights or targets potentially set for the features, and other considerations such connectivity. It therefore encompasses both the models that are used to produce the input data as well as details of prioritization analysis. The model can be relatively simple if, for example, the objective is to achieve a balanced representation of nominally different forest habitats. A more complex model could include additional components, such as accounting for similarity between habitats and habitat condition, and satisfying habitat-specific representation targets. The complexity of a model may be constrained by both the availability of suitable data and understanding of the ecological phenomenon involved. For example, the spatial distribution of a small and cryptic species may be largely unknown, and there may be incomplete information about the dispersal capability of a forest-dwelling species. Often the data ideally needed does not exist, in which case we often must use data surrogates and expert-opinion to fill in the gaps (Store & Jokimäki 2003; Ferrier & Wintle 2009).

Anything that we place conservation value on, can be used as a feature without requiring the feature to be a good surrogate for the occurrence of species *per se*, but in practice, the highest conservation value is frequently given to data that are well-known indicators or surrogates for other species and habitats. Forest biodiversity indicators can be classified into two categories: (i) compositional indicators directly measuring biodiversity, and (ii) structural indicators based on key structural features (such as average diameter and volume of trees) acting as correlates or surrogates for biodiversity (Corona et al. 2011). Compositional indicators are more accurate, as they measure biodiversity directly. Moreover, specific indicator or surrogate species are often used to represent a broader pool of species with similar habitat requirements (Similä et al. 2006; Grantham et al. 2010; Di Minin & Moilanen 2013). The problem with this approach is that direct, systematic observational data on the occurrence of species and habitats are rare, especially over broad spatiotemporal extents (Store & Kangas 2001; Sarkar et al. 2006; Moilanen 2012). Structural indicators are based on our ecological understanding on species and their habitat requirements (Lindenmayer et al. 2008). For example, many threatened species in Finnish boreal forests are dependent on specific structures and resources such as old trees and dead wood (Martikainen et al. 2000; Siitonen et al. 2000; Siitonen 2001, 2012) and measuring these features is almost always less laborious than observing species directly. However, structural indicators are useful only insofar as the truly correlate with the occurrence of focal species and empirical tests are required to establish these correlation (Lindenmayer et al. 2008).

What makes the approach based on structural features especially appealing is that many structural features are routinely measured or estimated as part of forest inventories (Tomppo 2006a; Chirici et al. 2011, 2012). Forest inventories provide data on the state of current forest resources and they are primarily used for forest management planning as well as national and international reporting. Many countries, including Finland, have implemented a system for a national forest inventory (NFI), providing systematically measured or estimated data over the whole country (Tomppo 2006a). Forest inventory data thus provides exciting potential for spatial conservation planning and I use forest inventory datasets extensively in this thesis.

1.5 OPERATIVE DECISION-SUPPORT FOR FOREST CONSERVATION IMPLEMENTATION

The scale at which spatial conservation can and should be done is a recurrent theme in this thesis. As stated in Subsection 1.3, spatial conservation planning is inherently a multi-scale activity, where assessments are done on a regional scale and conservation action is implemented at the local scale. Unfortunately, regional plans often translate poorly into local conservation action (Knight et al. 2008; Pressey et al. 2013). There are many reasons for this "knowing-doing gap" (Pfeffer & Sutton 1999), many of which are relevant for Finland as well. Organizations responsible for the implementation of conservation action may not be familiar with the best available scientific knowledge and develop and maintain their own approaches (Prendergast et al. 1999; Pullin et al. 2004). On the other hand, even if implementation is often considered at least from theoretical standpoint in scientific literature, the majority of conservation assessments published are not designed for implementation (Knight et al. 2008). According to Knight et al. (2006b), in order to be meaningful for general land-use planning, operational conservation planning should: (i) provide processes for forging close working relationships between conservation planners and land-use planners, (ii) educate land-use planners on the importance of maintaining regional-scale ecological function and techniques of systematic assessment, and (iii) complement data on priority conservation areas with interpretive information, training, and, if necessary, decision-support systems. While conceptually and methodologically my work is focused around spatial conservation prioritization – the assessment phase of conservation planning – these recommendations have certainly been leading principles in my work. I provide information on lessons learned in Section 4 of this thesis summary.

2 THESIS OUTLINE

In this thesis, I present five articles that collectively address the research objectives outlined in the previous section. My work fits into a broader context of conservation decision-making (Figure 1), which includes components and scientific disciplines such as ecology, conservation biology, decision-analysis, and forest management. I concentrate mostly on the conservation planning process involving the spatial allocation of conservation resources (quantitative spatial conservation prioritization). The fact that forest management and planning in Finland is highly effective and based on sophisticated information systems is a great opportunity for conservation science and implementation. Consequently, one further objective of my thesis has been making the approach developed adoptable by different organizations involved in planning and implementation of forest conservation and management in Finland.

In Chapter **I**, we introduce a novel approach in expanding the forest reserve network in Finland using forest inventory data, expert knowledge, and Zonation. More specifically, the objective was to find 10 000 ha worth of the most suitable reserve expansion sites on state-owned land. This is the first complementarity-based spatial prioritization (1.1) approach used at a broad extent in Finland. The ecological model underlying the prioritization approach was simple and implemented via a set of indexes of forest conservation value. This index relates structural forest inventory data, such as average volume and age, to an expert view how valuable different types and ages of forest for conservation. In the chapter, we develop and implement a new connectivity method in Zonation to simultaneously account for connectivity between multiple partially similar habitats (here forest types). In the end, we summarize an approach on how to expand the protected area network on state-owned land in south-central Finland, accounting for the spatial structure of the existing protected are network and what is already protected.

In Chapter **II**, we turn to the effects that data resolution and connectivity have on conservation prioritization results. High-resolution analyses can be computationally difficult or even unfeasible

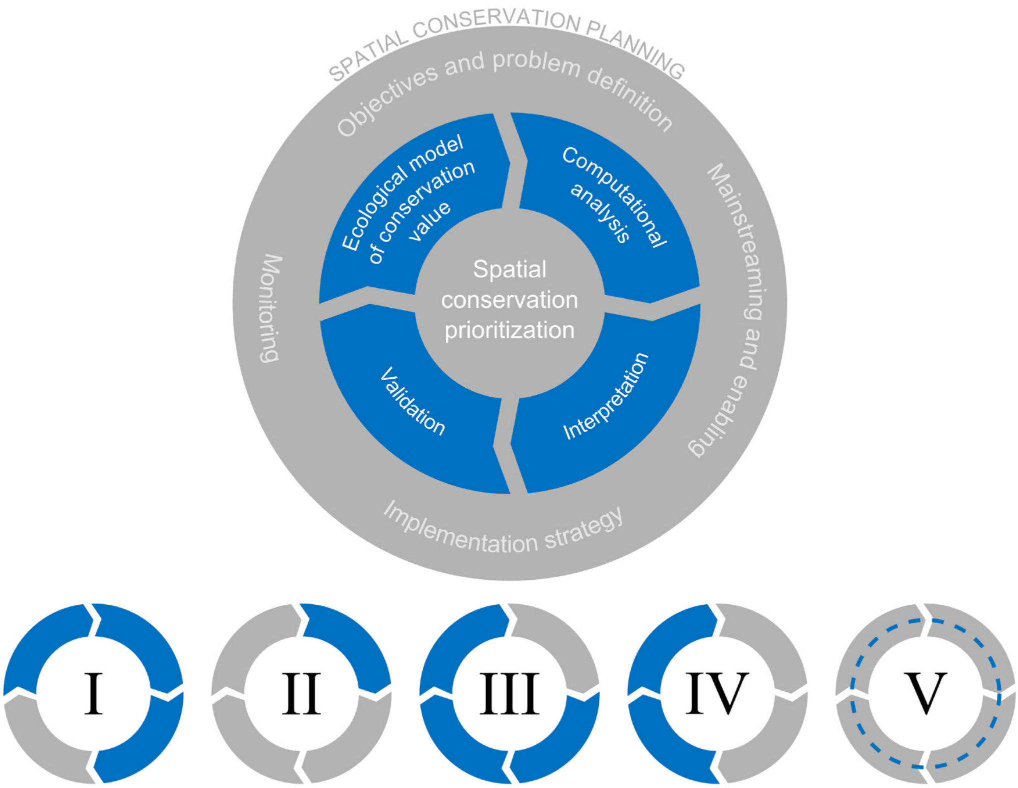

Figure 1. Schematic of the four high-level stages of spatial conservation prioritization and the contents of this thesis. The large inner circle (in blue) shows the stages in the order that typically occurs in a spatial conservation prioritization process. It also highlights the fact that the process is iterative over time. Note however, that in real life spatial conservation prioritization process rarely is a linear process: several feedback mechanisms exist between the different stages and the order of execution may vary somewhat end there may be iteration of stages. The large grey circle in the background represents the broader spatial conservation planning and decision-making context that defines the objectives and the constraints of the prioritization process. The smaller circles in the bottom show which stages of the process each chapter in this thesis addresses (see Section 2 for a complete thesis outline). Note also that Chapter **V** does not deal with any of the stages in particular, but rather with the whole process and workflow itself. *Ecological model of conservation* value refers to all the input data used, weights set to the features, and other analysis options (e.g. connectivity) that are included in the prioritization. *Computational analysis* deals with the computational and analytical aspects of spatial conservation prioritization as well as with methodological development (of Zonation, in the context of this thesis). *Interpretation* refers both to the interpretation of results as well as case-specific planning products such as refined rank priority maps and lists of potential sites for reserve network extension. *Validation* means assessing how the results compare against independent data sets that contain spatial information about known locations of high conservation value.

because of large spatial extents, high resolutions, and the large number of biodiversity features in which case aggregating the data and doing a coarse-resolution analysis may be a tempting alternative. However, the top regions identified using coarser data are not necessarily the same than when using high-resolution data. Furthermore, the solutions may be too coarse to be relevant for operative conservation planning. The approach introduced in Chapter **I** forms the basis of the analysis in Chapter **II**, which focuses on how similar – measured by both the spatial overlap and the rank correlation of the different solutions – the results are when we employ the same data at different resolutions and account for connectivity at ecologically relevant scales. We also introduce a new feature in Zonation that is able to better account for the aggregation of conservation value at edge areas that are known to be valuable (such as inland lake shorelines) or that have missing data in where there clearly should be habitat (such as national borders).

Validation of the prioritization results is an important, if frequently overlooked, part of the conservation prioritization process. All the analysis in Chapters **I**-**III** are based on a relatively simple model of conservation value. However, except for Chapter **III**, the validity of the results is not explicitly tested. In Chapter **IV**, we investigate how well prioritization analyses based on coarse inventory data perform when compared against same analyses based on more detailed inventory data. For validation, we employ locations of known valuable forest areas such protected areas and woodland key-habitats. The utility of prioritization analyses depends not only on the validity of the results, but also on the availability of the data. Open access to data would greatly enhance the utility of quantitative conservation prioritization tools and potentially the uptake of the results. The coarse data used in Chapter **IV** is open data whereas the more detailed is not. The chapter therefore seeks to better understand how useful open forest inventory data is in conservation prioritization in Finland.

Finally, in Chapter **V** we collate and discuss the best practices of planning and executing a conservation prioritization project using Zonation, which has become a powerful, but arguably complex framework for prioritizing many different types of conservation action (Box 2). The ecological model of conservation value underlies all prioritization analysis, but thus far, there has not been an explanation of what the model consists of and how one should construct such a model. In this chapter, we cover different stages of model construction. Furthermore, we give reasonable estimates on time and human resources needed and discuss the best- and worst-case scenarios for the different stages of the whole prioritization process. We also outline risks and benefits of spatial prioritization perceived by stakeholders.

All of the chapters in my thesis are relevant for operational conservation planning, and in fact, two of the chapters of this thesis have been instigated by actual real-life conservation planning problems (**I**, **IV**). Furthermore, regional environmental authorities almost immediately made successful use of the results presented in Chapter **III** in on-the-ground monitoring of the capercaillie. The non-scientific details and stages of conservation planning and implementation seldom make it into peer-reviewed publications (Knight et al. 2006a), but are interesting for conservation scientists and certainly for practitioners. I have tried to include as much of my personal experience in the results and discussion (section 4) as possible. I also formalize and present part of these experiences in Chapter **V**. Finally, I have included a subsection "Study context" (3.2), which introduces MetZo, a project that I have worked with extensively at same time as preparing this thesis. Furthermore, I also list other projects that are directly related to MetZo or that have applied similar approaches to conservation planning and implementation in Finland. I hope this section serves as an informative account of the context and the uptake of the approach presented in the chapters.

3 MATERIAL AND METHODS

3.1 STUDY AREAS

All my work has been done in Finland, a country with a total area of 338 000 km^2 spanning the northern latitudes of roughly 60°N to 70°N (Figure 2). Finland is a relatively flat country in terms of topography, and extensive and fragmented lake complexes characterize especially the central and eastern parts of the country. Climatically, Finland is part of the boreal zone with thin strip of the southern coast belonging to the hemiboreal zone. Finland's forests are mostly coniferous dominated by the Scots pine (*Pinus sylvestris*) and the Norway spruce (*Picea abies*) mixed with varying amounts of deciduous tree species such as the silver birch (*Betula pendula*), the downy birch (*Betula pubescens*), and the European aspen (*Populus tremula*).

The chapters of this thesis deal with different spatial extents ranging from regional to national (Figure 2). The national-level (**II**) covers the whole country including all the forest vegetation zones (hemiboreal, southern-, middle-, and northern-boreal, and hemiarctic) found in Finland. The study area in Chapters **I** and **III** follows the implementation area of the METSO-programme (Figure 2 and Box 2),

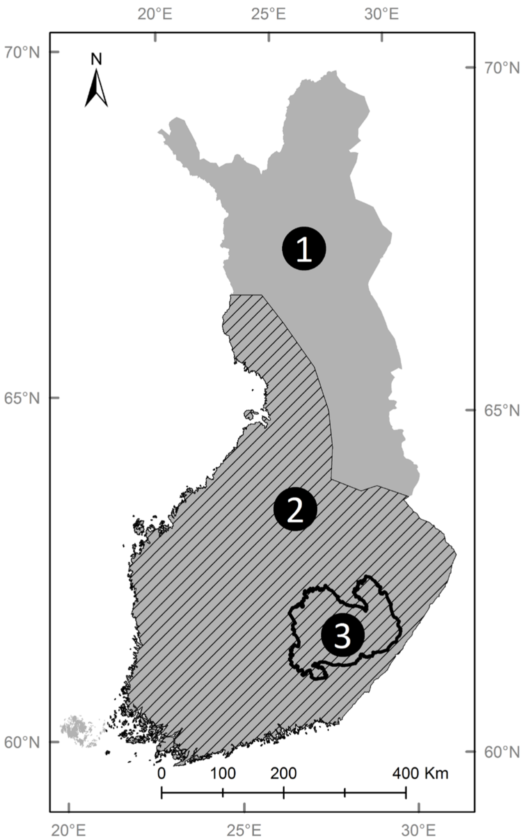

Figure 2. The study areas employed. 1 = The whole country, 2 = METSO-region, 3 = Southern Savonia.

which in itself corresponds roughly to the hemiboreal and southern- and middle-boreal forest vegetation zones. In Chapter **I**, the aim was to identify the most suitable reserve expansions on state-owned land for the implementation of the METSO. In principle, METSO also provides conservation management instruments for the capercaillie and therefore we used the same study area also in Chapter **III**. An additional reason for the chosen extent was that the METSO-region roughly corresponds to the part of Finland where the capercaillie is categorized as regionally threatened (RT; Rassi et al. 2010).

Finally, in Chapter **IV** we did all the work at the regional level in the province of Southern Savonia (Figure 2). Combined with the high resolution (60 m) used in the study, we were able to run prioritizations analyses that correspond, both in extent and in precision, to the needs of operative forest planning.

3.2 STUDY CONTEXT

Partly based on the work we did with Metsähallitus NHS (**I**) and FFC (related to **IV**), a new umbrella project called *Zonation Decision-Support for METSO* (**MetZo**) was initiated in spring of 2010. The project is funded by the Ministry of Environment, the Ministry of Agriculture and Forestry, the University of Helsinki, and the University of Jyväskylä. Other partnering organizations include Metsähallitus NHS (which also coordinates the project), the Finnish Environment Institute (**SYKE**), the FFC, Metla, ELY Lapland, and Tapio Forestry Consulting .

The objectives of MetZo can be divided into two categories. First, MetZo produces information that directly supports the operative planning and implementation of the METSO-programme (Box 2). In practice, MetZo identifies spatial conservation priorities in forest and peatland ecosystems. Additionally, MetZo aims at capacity building within and knowledge transfer between the partnering organizations. Second, MetZo has several research and development objectives. For example, active research is being done on applying the prioritization approaches using Zonation to particular environments (such as peatlands) and in exploring ways of integrating several different environments in a single analysis. Developing a common data and computational infrastructure is also an important objective. The project runs until the end of 2014.

Since 2010, I have partly funded by the MetZo-project. I have lead the subgroup working on forest environments and much of the work in this thesis has been done in the context of MetZo. In addition to the research and development, work in MetZo has involved public outreach, organizing stakeholder workshops, and training events in the project partner organizations.

In addition to MetZo, several other projects (Table 1) in spatial conservation prioritization have taken place during the time it took for me to finish this thesis. Not all are directly related to MetZo, but

Table 1. Research and implementation project using Zonation for spatial conservation prioritization in Finland. Not all projects are forest-specific, but all have either an ecological or an administrative link to forests. Projects in bold are directly related to the MetZo-project.

Project	Extent	Year	Aims	Organizations	Reference
METSO 10 000	METSO	2008-2009	Expanding protected area network on state-owned land (10 000 ha).	Metsähallitus NHS UH	Chapter **I**, http://bit.ly/metzo10k
GIS methods for biodiversity conservation in commercial forest landscapes	Southern Savonia	2009-2012	Promoting biodiversity in commercial forest planning.	FFC UH	Chapter **IV**
Forestry-Zonation	METSO	2010-2013	Outreach and mainstreaming of the spatial conservation prioritization in forest planning.	Tapio FFC UH	http://bit.ly/forzo (in Finnish)
Most valuable large natural or semi-natural peatlands	METSO	2011-2013	Identification of valuable peatlands.	SYKE UH Metsähallitus NHS	-
Targeting the monitoring effort of capercaillie	METSO	2012-2013	Introduce a practical tool for large-scale management for capercaillie lekking landscapes in Finland.	UH FRGRI ELY Uusimaa	Chapter **III**
Natura 2000 management landscapes	Finland	2012-2013	Identification of top priority areas and management landscapes from a national Natura 2000 network.	Metsähallitus NHS UH	Mikkonen & Moilanen (2013)
Targeting of peatland conservation and peat extraction	Central Finland	2012-2013	Use of inverse spatial conservation prioritization to avoid biological diversity loss outside protected areas.	JyU HU Regional authorities	Kareksela et al. (2013)
Connectivity and agro-environment schemes	Satakunta region	2012-2013	Improving conservation planning for semi-natural grasslands: Integrating connectivity into agri-environment schemes.	HU SYKE	Arponen et al. (2013)
NATNET-Life+	Southwestern Lapland	2012-2016	Increasing the ecological connections and coherence of the Natura 2000 network in Southwest Lapland.	ELY Lapland FFC Metla Metsähallitus NHS Metsähallitus FOR	In progress, http://en.natnet.fi/

MetZo-hallitus	METSO	2013-2014	Expanding protected area network on state-owned land (15 000 ha).	Metsähallitus NHS Metsähallitus FOR	http://bit.ly/metzohallitus, (in Finnish)
Spatial conservation prioritization in zoning and general land-use planning in Uusimaa region	Uusimaa region	2013-2014	Green infrastructure and biodiversity in general land-use and zoning.	URC HU	In progress
Complementing national peatland PA network	Finland	2014	Assessing and prioritizing candidate peatland sites to expand to protected area network by 100 000 ha.	ME SYKE UH Metsähallitus NHS	In progress
Broad scale forest conservation priorities and landscape corridors	Finland	2014	Identifying broad-scale forest corridors within Finland while accounting for connectivity in to neighboring countries.	SYKE UH	In progress

Table 1 does give an overview of the extent to which spatial conservation prioritization and Zonation are being studied and applied in Finland.

3.3 DATA

3.3.1 Forest inventory data

The chapters of this thesis make extensive use of data produced by three different forest inventory systems: the multi-source national forest inventory (**MS-NFI**), and the forest inventory systems of the Finnish Forest Center (**FFC**) and Metsähallitus NHS. As many of the chapters are partly based on the same data, I will provide here an overview of the three different inventories.

The multi-source national forest inventory is a method and data developed in the Finnish Forest Research Institute Metla for estimating forest resources at the local level based on the National Forest Inventory (**NFI**). The NFI is a sampling-based inventory system maintained by Metla, which covers all land-use classes and ownership categories throughout the whole country (Tomppo 2006a; Tomppo et al. 2008; Tuominen et al. 2014). The primary objective of the NFI is to provide reliable information on forest resources and biodiversity for forest planning and management at national and regional levels (Tuominen et al. 2014). The MS-NFI method employs statistical estimation based on non-parametric *k*-Nearest Neighbor method, satellite images, digital maps, and NFI field measurements to estimate thematic digital maps about structural features of the forest across Finland at a detailed spatial resolution of 20 meters. The thematic maps produced contain over 40 forest variables, including for example the volumes by tree species, stand mean variables, the biomass by tree species groups, and forest site type characteristics (Tomppo 1990, 2006b; Tomppo et al. 2008). In Finland, the MS-NFI is mostly used for regional level forestry planning. We use the MS-NFI data in Chapters **I**-**IV**.

Several authors have used NFI data for spatial conservation planning in Finland before. Luque and Vainikainen (2008) developed a tool for reserve area extension by using data from from the NFI and the MS-NFI over the whole METSO region (Box 2). They used forest features, such as the average volume and age of trees, combined with expert knowledge to create threshold-based habitat quality models. Their approach also accounted for the proximity of existing reserves. Habitat quality indexes were then used to identify areas of highest conservation potential. Kallio et al. (2008) built upon the habitat quality models created by Luque and Vainikainen (2008) and used the model outputs in a spatial partial equilibrium model again to identify optimal sites for reserve network expansion while accounting for the economic impacts on the forest sector. Finally, Juutinen et al. (2008) developed a single habitat quality model based on MS-NFI features in the Satakunta region of Finland. They then studied how different threshold values for components of forest structural elements would influence cost-effective site selection. In their specific case, loosening ecological criteria could considerably lower the costs while sacrificing only limited ecological gains.

The FFC is a national forest authority that provides forest management guidance to forest owners and enforces the laws regulating commercial forestry in private forests. To support these roles, the FFC maintains the forest resource inventory system that covers approximately 59% of private forestry land in Finland (**PriFRI**). Similar to the MS-NFI, the main purpose of the FRI is to provide information on forest resources and biodiversity for forest planning and management. Before year 2011, forest structural and site type attributes were recorded at the stand-level based on visual assessments or on plot-based measurements. After 2011, the FFC has migrated to a stand-level system based on a statistical estimation from a combination of sampling-plots and remote-sensing. In the new system, stands are field-inventoried only if their attributes cannot be reliably estimated. Stand-level information is updated at least once per decade or whenever forestry operations are implemented. We use the FRI data in Chapter **III**.

Metsähallitus (the Finnish Forest and Park Service) is responsible for managing all the state-owned forests, both protected and commercially managed. Metsähallitus is further divided into two units: Metsähallitus Forestry (**Metsähallitus FOR**) manages commercial forests, and Metsähallitus Natural Heritage Services (**Metsähallitus NHS**) provides public administrative services such as the management of statutory protected areas and other areas reserved for conservation. In chapters **I** and **V** of this thesis, I have used data only from Metsähallitus NHS as Metsähallitus FOR did not grant access to its data. These data from Metsähallitus NHS constitute of two different inventories: the forest resources inventory data for public land (**PubFRI**), and the nature-type inventory (**NTI**). The PubFRI is very similar in structure and purpose to the PriFRI, although Metsähallitus NHS does not do forestry planning or management. The NTI, on the other hand, is designed more for biodiversity maintenance and management and it only covers the currently protected areas. It includes stand-level information about forest types, vegetation cover, the amount of dead wood, and general "naturalness" of forest. This information is missing in the more forestry-oriented inventory databases. We use NTI in Chapter **I** and the PubFRI in Chapter **IV**.

3.3.2 Habitat quality indices

Chapters **I**-**IV** of this thesis rely on expert knowledge in the construction of the ecological model of conservation value (see 1.4). The first component of the model is identifying which are the relevant factors for the prioritization problem at hand followed by the collation of information on the identified factors (Ferrier & Wintle 2009). In Chapter **I**, the objective of the spatial prioritization is to identify the best forest areas for expanding the reserve network on state-owned land in the context of the METSO-programme. Meetings held with regional and local expert from Metsähallitus established, that the new protected areas should be structurally mature or old. We then derived a simple index of the following form:

$$I_i = \sqrt{age \ x \ volume} \quad (1)$$

where I is the index value for a cell in location i (see also Figure 3). Note that several of these indexes are computed independently for different tree species occurring on variably productive land. This formulation gives higher index values to forest areas with a large volume of old trees.

Based on several workshops held with various experts (see 3.5.2), we further developed the habitat quality index (**III**, **IV**):

$$I_i = f\,(diameter) \times volume \quad (2)$$

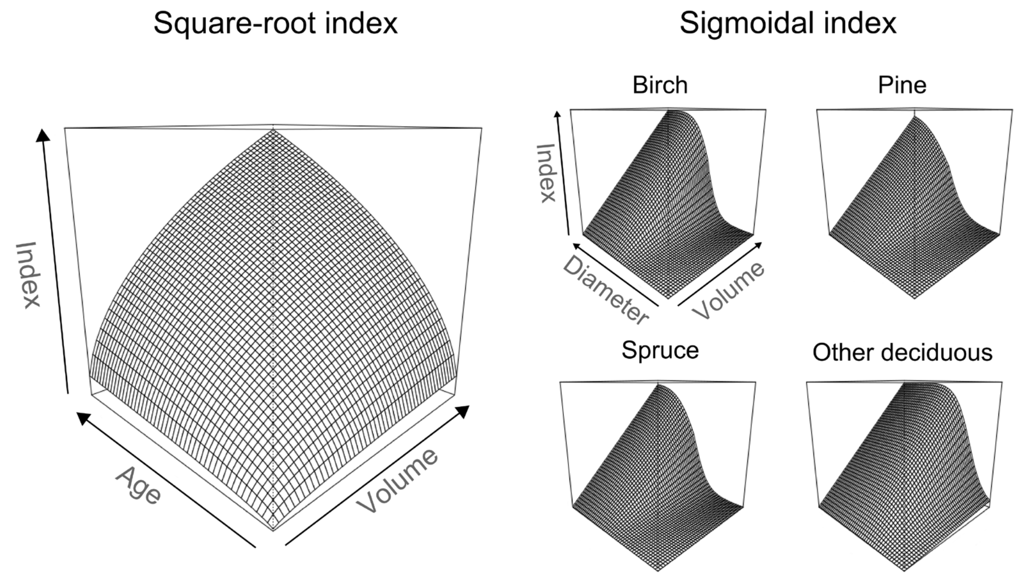

Figure 3. The effect of different components of the conservation value index. Plot on the left show how the square-root index (see text) used in Chapters **I** and **II** is related to average forest age and volume for all tree species. Plot on the right shows the same for the sigmoidal-index (see text) for different tree species groups used in Chapter **IV**. A modified version is used in Chapter **III**.

where *I* is the index value for a cell in location *I*, and *f* is a specific sigmoidal function that translates the average diameter (a proxy for maturity) into a multiplier for volume. The rationale behind the sigmoidal shape of the function is that it gives little value to relatively low diameter trees, after which and when approaching a preset inflection point the value increases relatively quickly. Finally, the increase levels off as high enough average diameter values are reached. Again working with experts, we constructed specific sigmoidal functions for each main tree species group (birch, pine, spruce, and other deciduous; see Figure 3) which we parameterized differently to reflect how habitat quality increases within each group. For example, other deciduous trees generally are more valuable to conservation at younger age than pine. In Chapter **III**, we constructed the sigmoidal functions to correspond with what is known about the habitat requirements of focal-species, the capercaillie. In Chapter **IV**, the functions reflected what the experts generally regarded as valuable for conservation as well as the empirical distribution of average diameter and volume records in the input data.

It is worth noting, that both index formulation presented above are very simple in structure designed to give more value mature forests. Because of the formulation, several forest habitat types, such as rocky outcrops with forests, and several different peatland habitat types, such as spruce mires, might receive relatively low value. Furthermore, relying on volume may give too high value on commercially managed stands.

3.3.3 Validation data

We validated the results of the prioritizations in Chapters **III** and **IV** by examining the priority distributions within independent spatial datasets, which are known to have higher than average conservation value.

In Southern Savonia (**IV**), we used three different validation data sets. First, we used the database on established protected areas maintained by Metsähallitus NHS. Protected areas also cover mires, but for validation, we used only protected areas on mineral soils (~1.9% of the whole landscape in Southern Savonia). Second, we acquired the known locations of woodland key-habitats (**WKH**), which are small habitat patches of especially high conservation value (Timonen et al. 2011) . On average, WKHs house more dead wood dependent and red-listed species, and have higher species richness than the surrounding commercially managed landscape (Timonen et al. 2011). Third, we used the spatial delineation of sites that have recently been acquired by the METSO-programme. The sites selected in METSO are ecologically valuable than average Finnish forest containing more dead wood as well as many red-listed species (Siitonen et al. 2012). We used only areas with permanent conservation contracts for validation, as the conservation effectiveness of temporary or fixed-term contracts is questionable (Siitonen et al. 2012).

We used the known location of 448 capercaillie lekking sites in Central on Southwestern Finland to validate the Zonation prioritizations (**III**). These data were collected by the Finnish Game and Fisheries Research Institute, by local experts, by the ELY Centre Uusimaa, and by questionnaires and interviews from local game management personnel, landowners and hunters (**III**).

3.4 DATA PRE-PROCESSING

In order to convert the input data into input features for Zonation, a sequence of pre-processing stages is required in each of the Chapters I-IV. These stages are essentially geoprocessing operations that I have done inside a GIS or by using other programmatic geospatial processing tools. Out of the forest inventory databases described in Subsection 3.3.1, the MS-NFI, is natively in raster format with resolution of 20 x 20 meters. All the other inventory systems are based on a relational spatial database, where a number of attributes (such as the average volume and diameter) are linked to a particular spatial feature i.e. a forest stand. Zonation requires that all the input data is in raster format as well as that all the rasters have the same spatial resolution (20 x 20 m) and extent. Therefore, the first stages of pre-processing involved the following steps:

1. Selection of the spatial features (i.e. forest stands) that are to be included classified by the dominant tree species group.

2. Relating the selected attributes with the spatial features.

3. Rasterizing the vector data using a fixed spatial extent (that of the MS-NFI data) and resolution (20 x 20 m).

Describing spatial features that are smaller than the resolution used may lead to a problem of mixed pixels (Fisher 1997; Cracknell 1998), where the some of the features might be misrepresented by the resolution used. Therefore, using datasets with different structure required us to consider potential problems associated with rasterizing. In our case, the minimum spatial resolution is bound to the resolution used in the MS-NFI data. The minimum mapping unit in the original vector data is forest stand, which most of the time can be reasonably well represented by 20 x 20 m pixels.

Note that all the rasterized data had already been categorized according to the dominant tree species group (birch, pine, spruce, and other deciduous). If there are n attributes that are related to the same spatial feature (a single stand has information on both the average volume and the average diameter), then the steps given above will have to be repeated 4 x n times. After these steps, input data from all the different inventory sources are in the same format.

The next steps of pre-processing involved the construction of the habitat quality indices. In generalized form, the sequence of operations was the following:

4. Applying an index transformation on each raster (see 3.3.2 and Figure 3).

5. Splitting the index rasters according to the site fertility class.

6. Aggregating the index rasters up from 20 x 20m resolution into the desired analysis resolution using sum as aggregation statistic.

In step 5, we split the index rasters into further categories based on 5 site fertility classes. Therefore, in the end we were left with 4 x 5 = 20 different index rasters. Note that in chapter IV the pre-processing sequence is more complex, because we are combining data from all of the different forest inventory databases.

In step 6, several factors had to be considered when aggregating data from higher to lower resolution. Changing resolution may give rise to artificial spatial patterns or changes in the statistical properties of the data, an issue described as the ecological fallacy (Gotway Crawford & Young 2004) or the modifiable areal unit problem (MAUP)(Openshaw 1984; Jelinski & Wu 1996). Aggregating the habitat quality indices was, however, fairly straightforward as we were dealing with continuous values.

The steps described above apply to the structural attributes in the forest inventory databases, which are needed to calculate the index for habitat quality. There are, however, other types of data included in the chapters. Chapter I makes use of the NTI (3.3.1) data describing the occurrence of valuable habitats within protected areas, and Chapter III includes land-cover data indicating human influence that has negative influence on the occurrence of the capercaillie. For these data, the pre-processing steps are generally the same without steps 4 and 5.

We implemented part of the pre-processing steps as ArcGIS (ESRI 2014) toolbox called *zupport* that was deployed into the information system in the FFC (IV). The development version is also available in GitHub (https://github.com/cbig/zupport). The habitat quality index computations were implemented using custom-made geospatial scripts based on Python (Python Development Team 2014) bindings to GDAL (GDAL Development Team 2014). The implementation is available in GitHub (https://github.com/jlehtoma/zsetup-esmk/preprocessing/python).

3.5 SPATIAL CONSERVATION PRIORITIZATION USING ZONATION

3.5.1 Computational analysis

In Chapters **I**-**IV**, I use a particular approach for quantitative spatial conservation prioritization: Zonation. The Zonation framework and software (Moilanen 2005; Moilanen et al. 2009b, 2014) are intended for quantitative conservation prioritization across large landscapes using input data describing the distribution of biodiversity features such as species (Leathwick et al. 2008; Meller et al. 2014), communities (Arponen et al. 2008; Moilanen et al. 2011b), habitat types (Klein et al. 2009; Kareksela et al. 2013), and ecosystem services (Moilanen et al. 2011a). Features can be weighted differently reflecting for example conservation preferences. Starting from a full analysis area formed by the input feature rasters, Zonation proceeds by iteratively removing the least valuable cells accounting for factors such as occurrence of features in the cells, the remaining occurrence level of each feature across the whole area, and connectivity within and between features. At each iteration, the features are normalized by their remaining range-size, meaning that as a feature becomes rarer during the cell-removal process, its relative significance increases. Put differently, Zonation removes cells with low feature richness and cells with occurrence of features with low weights and extensive distributions. The repeated range-size normalization (Moilanen 2005; Moilanen et al. 2009b) leads to maintenance of a balance between all features at all iterations. What exactly is considered the "least valuable cell" depends on multiple factors, and not least on the so-called cell-removal rule, which specifies how (loss of) conservation value is integrated across multiple features and space. Chapter **V** gives and overview of Zonation's main capabilities.

Zonation produces a set of standard outputs. The most commonly seen output is the rank priority map. Zonation produces a nested ranking of all the cells with value of 0 indicating the lowest and 1 the highest priority, with nestedness referring to the fact that the top 1% is always contained within the top 5%, which is contained within the top 10% and so on. The nested ranking is often visualized by different color schemes for visual interpretation (**I**-**IV**), but the rank priority maps are in fact numeric rasters that can be analyzed in many quantitative ways as well (**I**-**IV**). Another main – and equally important – output of Zonation are the so called performance curves (**I**, **II**, **IV**, **V**). The curves quantify the proportion of the original occurrences remaining for each feature when successively smaller fractions of area of analysis remain in the process (it is implicitly assumed that a given top fraction is designated to conservation and that the rest might be lost). These curves can be very useful in answering questions like "How much of the occurrence of each biodiversity feature can we cover by protecting, say, 10% of the landscape?"

In most of the chapters (**I**-**IV**), we include connectivity by using the distribution smoothing (**DS**) method in Zonation, which is a metapopulation-type connectivity measure implemented as a radially symmetric negative-exponential (i.e. connectivity effect decreases by distance) dispersal kernel (Moilanen 2005; Moilanen et al. 2005). Whereas the conventional DS method in Zonation applies the connectivity transformation to a single biodiversity feature at a time, in Chapter **I** we introduce a new many-to-one version of the DS method (dubbed "matrix-connectivity") which enables us to account for connectivity between many different biodiversity features simultaneously, given that the connectivity coefficients between the features can be quantified. The second connectivity method we employ in Chapters **I** and **III** is the so called connectivity interaction method. This method is either a positive or negative connectivity interaction between a pair of features where the interaction originates from one of the features and affect the other (Rayfield et al. 2009). An example of positive interaction is proximity to existing protected areas (**I**), whereas a negative interaction is exemplified by the avoidance of human-impacted areas (**III**).

The features and flexibility of Zonation make it a suitable tool for e.g. operational land-use planning (Gordon et al. 2009; Thomson et al. 2009; Carroll et al. 2010), but as with any other computational tool it comes with limitations. Zonation is not the right tool for all types of conservation and land-use planning, but it can be used to complement other tools in more complex planning situations. For example, RobOff (Pouzols et al. 2012; Pouzols & Moilanen 2013) is a software tool designed for analysis of alternative land-use and conservation actions. RobOff can be used to study the potential effects of e.g. restoration actions over time, but unlike Zonation, it is not spatially explicit. Combining the two tools (Zonation and RobOff) can be used to select best combination of actions and to target them in certain regions (Maggini et al. 2013). Chapter **V** introduces several other conservation planning tools and their differences and similarities to Zonation as well as some of the limitations it has.

3.5.2 Expert participation, weights, and connectivity

The term "expert" is commonly used to refer to a wide array of professionals from various fields and organizations ranging from scientists to practitioners and stakeholders (Perera et al. 2012). Experts hold information about a given topic and experts are frequently deferred to on matters that involve the interpretation of this information (Barley & Kunda 2006). The knowledge of experts can be acquired by training, research, and skills, or through personal experience (Burgman et al. 2011; Martin et al. 2012). In fields such conservation management, where decision need to be made urgently and often without sufficient empirical evidence, expert judgments are regularly used to support decision-making (Martin et al. 2012). The chapters of this thesis use expert knowledge extensively especially in regards to constructing the ecological model of conservation value. Furthermore, while the objectives of spatial conservation planning stem from high-level objectives (such as the METSO-programme), experts are needed to formulate the low-level operative objectives.

The experts I have worked with in this thesis mostly come from publicly funded research and management organizations, and from the Finnish environmental administration (Table 2). I have done part of my work (**I**, **IV**) as part of larger implementation-oriented projects (see 3.2), and thus the chapters do not fully describe the expert-work involved. We typically first assembled a core-team of researchers and experts, and worked together to define the exact research questions involved and which decisions the prioritization is exactly supposed to inform. After we

Table 2. Spatial conservation prioritization options used in different chapters. Chapter **V** is omitted, as it does not introduce new analyses. For detailed technical description of methods and parameters used in Zonation, see Moilanen et al. (2014).

	I	II	III	IV
Extent[1]	METSO	Finland	METSO	Southern Savonia
Data[2]	MS-NFI + NTI	MS-NFI	MS-NFI	MS-NFI + PubFRI + PriFRI
Resolution	300 m	100, 200, 400, 800, 1600, 3200, 6400, 12800, and 25600 m	100 m	60 m
Index[3]	Simple square-root index	Simple square-root index	Sigmoidal index adjusted for the capercaillie	Sigmoidal index adjusted for general forest conservation value
Zonation				
Cell-removal rule[4]	ABF	ABF/CAZ	ABF	ABF
Connectivity[5]	MC + IA (positive)	MC	MC + IA (negative)	MC
Distances	DS: 2km, IA: 5km	DS: 1, 2, & 4km	DS: 0.2, 2, & 10km, IA: 0.5km	DS: 2km
Features[6]	BD	BD	BD + TH	BD
Weights	Expert-opinion	Equal weights	Expert-opinion	Expert-opinion
Informative cells	2.3 million	28 million	18 million	3.8 million
Results interpretation	- Visual comparison - No. and mean size of sites - Spatial overlap of solutions - Performance curves	- Visual comparison - Spatial overlap of solutions - Rank correlation	- Visual comparison - Spatial overlay analysis	- Visual comparison - Spatial overlap of solutions - Replacement cost analysis
Validation	-	-	Species Data	PAs
Expert participation[7]	- Metsähallitus NHS - Metla	- Metsähallitus NHS - Metla	- FGFRI - ELY Uusimaa	- FFC - Metla - Metsähallitus NHS - Metsähallitus Forestry - SYKE - ELY Southern Savonia
Used on-the-ground	X	-	X	X

1: See also Figure 2.
2: See 3.3.1 for the explanation of the abbreviation and detailed description.
3: See 3.3.2 for details on the indices.
4: ABF = additive benefit function; CAZ = core-area zonation
5: MC = Matrix connectivity, or a many-to-one version of distribution smoothing connectivity method available in Zonation (see Chapter **I**); IA = interaction connectivity (either positive or negative).
6: The type of features used in the ecological model of conservation value (see 1.4). BD = biodiversity features; TH = threats.
7: FFC = Finnish Forest Centre; Metsähallitus NHS = Metsähallitus Natural Heritage Services; Metla = Finnish Forest Research Institute; ELY = Centre for Economic Development, Transport, and the Environment; FGFRI = Finnish Game and Fisheries Research.

had a good idea on the goals and constraints of the prioritization, we then moved on to construct the ecologically based model of conservation value. This typically meant involving a wider group of experts and organizing stakeholder workshops. For example, the largest workshops we held in Southern Savonia (**IV**) had approximately 20 participants representing also private forest owners and their associations.

The core-teams were mostly responsible for defining the overall structure of the ecologically based model for conservation value. This included defining the relevant input datasets and pre-processing steps to create the biodiversity features for Zonation (see 3.3.2 and Figure 4), as well as defining roughly what the weights should be and what types of connectivity methods are used. Table 2 summaries the ecological model of conservation value and some Zonation-specific parameters used in the chapters of this thesis.

For example, we established with the experts from Metsähallitus (**I**) that more weight in the analysis should be given to herb-rich forests and fertile sites, because these types of habitats are generally considered as the most valuable and species-rich (Virolainen et al. 2001; Heikkinen 2002; Rassi et al. 2010). Working with a different set of experts (**III**), we built another weighting scheme base both the scientific literature and expert-opinion to reflect the habitat requirement and preferences of the capercaillie. For Chapter **IV**, the weighting scheme

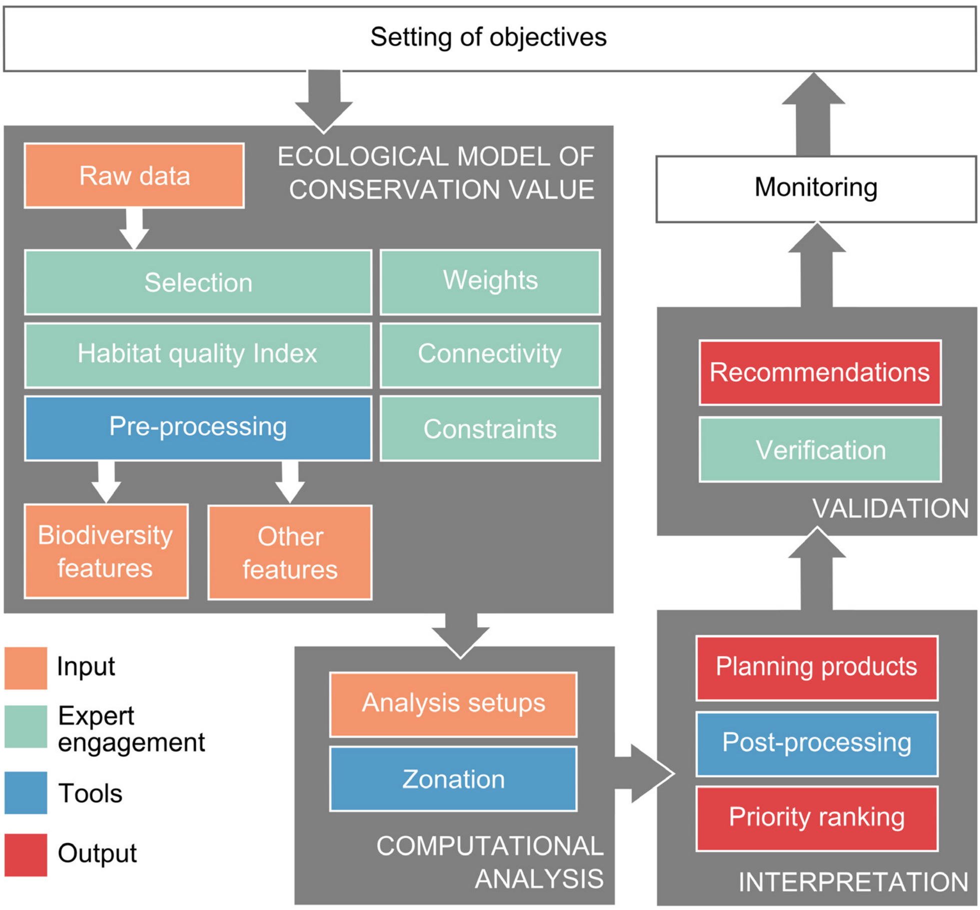

Figure 4. A schematic of the stages of a spatial conservation prioritization process (adapted from V). Groups defined by the gray background correspond to the four high-level stages in Figure 1. Orange color indicates inputs to other stages of the process. Light green color indicates active operations, that include engaging with experts. Blue color indicates stages, where computational tools are employed. Red color indicates outputs from other stages of the process.

was initially created by the core-team and refined later as a result of a larger stakeholder workshop.

We also engaged with experts in defining the relevant scales of connectivity. While we have a reasonably good understanding on the spatial ecology of some forest species (such as the capercaillie, **III**), for the majority we do not have empirical data with which to work. Research done in boreal forests on for example on polypores (Edman et al. 2004; Norros et al. 2012; Nordén et al. 2013), insects associated with polypores (Jonsson & Nordlander 2006), and the flying squirrel (*Pteromys volans*)(Selonen & Hanski 2004) gives indications to particular dispersal capability of 1-5 km. In addition to the ecological reasons, connectivity can be a desirable feature considering conservation action, i.e. it is more cost-efficient to aggregate conservation actions for example on the regional scale. Eliciting connectivity-related information from the experts required a fair amount of communication between the researchers and experts involved. We had to make sure that it is conceptually clear what we mean by connectivity, and how the actual distance measures we were interested in relate to these concepts.

3.5.3 Analysis setups

Designing the ecological model of conservation value (see 1.4), a prerequisite for a Zonation analysis, can include a formidable amount of work. All Zonation capabilities are documented either in peer-reviewed literature (3.5.1), in the technical manual (Moilanen et al. 2014), or in a relatively recent introductory guide (Di Minin et al. 2014). Nevertheless, setting up an analysis without previous experience is challenging simply due to the array of options available and the multitude of Zonation input and configuration files.

Analysis setups refers to all input, configuration, and control files needed to execute a Zonation run (i.e. a single analysis). For complicated analyses, a good strategy is to construct the analysis sequentially (**V**) by starting from a very simple setup and including analysis features (e.g. weights, connectivity) one by one. In this way, it is easier to verify that the analysis works like expected and the results are reasonable (note that this is different from actual validation). Sometimes each such stage is called a *variant*. In the end, analysis setups constitute of several variants and all the associated files.

3.6 POST-PROCESSING

The standard outputs produced by Zonation are informative, but technical. The Zonation graphical user interface has several facilities to plot and analyze for example the rank priority maps and performance curves (3.5.1). However, often more fine-grained and flexible analysis of the results is needed. To facilitate the analysis of Zonation results, I created a package for the popular R programming language and statistical environment (R Core Team 2014). The package, called *zonator* (https://github.com/cbig/zonator), is designed to help users in the creation of Zonation setups (3.5.3) and in analyzing and visualizing the results. As an example, the analysis and visualization of the results in Chapter IV were implemented using zonator. The implementation is available in GitHub (https://github.com/jlehtoma/validityms/tree/master/src).

4 RESULTS AND DISCUSSION

Here, I present the most relevant findings of this thesis and discuss how these findings relate to the thesis objectives I presented in Section 1. The section is divided roughly into two parts. First (4.1, 4.2, and 4.3), I will present and discuss results of the prioritizations in Chapters **I**-**IV** in terms of the ecological models for conservation value (1.4) I have used. To reiterate, this includes investigations of the extent and resolution of the input data, the performance of the habitat quality indices, and other components of the spatial conservation prioritization such as weights and connectivity. Importantly, I will first show that habitat quality indices based on forest inventory data collected primarily for forestry planning can be used for well-informed conservation prioritization. This is conditional on the fact that the data used is available at the relevant spatial resolution and detail, as I will show in 4.2. I will conclude the first part by showing how connectivity can be used to emphasize large, continuous forest areas or to locate potential areas for reserve network expansions (4.3). Doing so will, however, inevitably happen at the expense of high-quality but isolated sites.

Box 3. Sections addressing the thesis study questions and objectives.

1. How suitable are commonly available forest inventory data for informative high-resolution conservation prioritization in Finnish forests?

Subsections: 4.1, 4.2, 4.4

2. To dissect the effects of scale and connectivity on spatial conservation prioritization at regional and national extents.

Subsections: 4.2, 4.3

3. To develop, demonstrate, and implement a practical workflow for regional- and national-scale forest conservation management planning in Finland.

Subsections: 4.1, 4.4, 4.5, 4.6, 4.7

In the second part (Subsections 4.4, 4.4, 4.5, and 4.7), I will turn to the more implementation-oriented objectives of this thesis. More specifically, I will address the factors identified in chapters **I**-**V** that are relevant for integrating spatial conservation prioritization into general forest management and planning. As I will show in the first part, the broad-scale patterns of conservation priorities are not confined by any particular legal or operative designation (e.g. is the forest protected or is commercially managed) or land-tenure (i.e. publically or privately owned forest). Therefore, the only way towards more extensive and effective conservation prioritization is through integrated forest management planning. I will then discuss the role of experts in the prioritization process, the prioritization process itself. Finally, and concluding the second part, I will argue that open access to best available data enhances the prioritization results, and that sharing the technical implementation of the analyses is important.

4.1 PRIORITIZATION BASED ON FOREST INVENTORY DATA CAN PRODUCE INFORMATIVE RESULTS

Habitat quality indices based on the forest inventory data form the foundation of the ecologically based models of conservation value (1.4) and thus the priorities produced by Zonation. Validation against independent spatial datasets reveals that the indices do indeed produce informative priorities (**III**, **IV**). Figure 5 illustrates part of the results of the validation procedure used in chapter **IV**. We examined the rank priority distributions within a set of spatial validation data that we assume should have higher than average conservation value. In other words, we expect that, for example, protected areas should receive higher than average priorities if the habitat quality index and

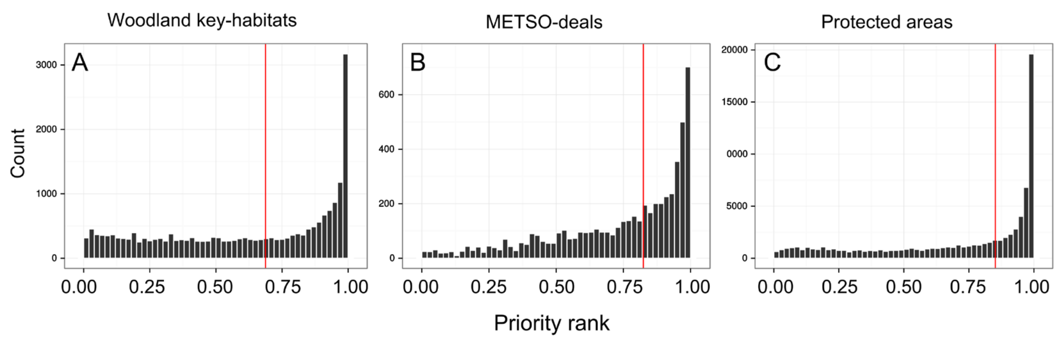

Figure 5. The priority rank distributions compared to independent spatial validation data in Southern Savonia (adapted from **IV**). Panel **A** shows the priority distribution within woodland key-habitats, panel **B** within recently closed METSO-deals (Box 2), and panel **C** within protected areas (see 3.3.3). Red vertical line corresponds to the median value. The high median value and high frequencies of top-priorities show that the analysis (**IV**) is able to identify forest sites with high conservation value.

the ecologically based model for conservation value truly work. All validation datasets have high median priority and furthermore the priority distributions peak at the absolutely highest priorities. We can therefore conclude, that our approach is capable of identifying forest areas of high conservation value, at least when value is defined relative to existing protected areas.

Prioritization based on forest inventory data is also informative for single-species management, as we show in Chapter **III**, where we identified potential lekking landscapes for the capercaillie. As explained in sections 1.4 and 3.5, if the ecologically based model for conservation value can be constructed in steps to study the effect of each added component (e.g. weights or a particular connectivity method). Depending on the objectives of the prioritization, more complex models should usually better correspond to the overall objectives and thus be more informative. We built the prioritization based on the MS-NFI data, population connectivity at multiple scales, and avoidance of human-impacted areas (negative connectivity). As a validation procedure, we compared the resulting rank priority maps to known capercaillie lekking-sites. The ecologically based model of conservation value worked relatively well even when connectivity and human-avoidance were not accounted for (Figure 5 in **III**). Including the spatial consideration (connectivity on multiple scales and human-avoidance) clearly improved the results, as the average priority within a 500 meters buffer around a known lekking-site increased from 0.66 to 0.78 (Zonation priorities range linearly from 0 [the least important] to 1 [the most important], or, equivalently, from 0 to 100% of the landscape). At the same time, the fraction of priorities within the buffers belonging to the best 20% of the whole analysis area increased from ~14% to ~49%.

The greatest potential to protect relatively mature herb-rich or herb-rich -like forests within the METSO-region (Figure 2) is on private land (**I**). Similarly, these forest types are currently underrepresented in the protected area network. Given the underlying ecological model of conservation value, the best candidates for expanding the protected area network on state-owned land are found in Central Finland, Northern Savonia and Northern Karelia. These regions contain the majority of herb-rich forests (Hokkanen 2003; Kallio et al. 2008; Finnish Forest Research Institute 2013), the most species-rich forest environment in Finland (Virolainen et al. 2001; Heikkinen 2002; Rassi et al. 2010). Working together with the experts from Metsähallitus, we produced an informative conservation prioritization that was used in implementing a ~10 000 ha expansion of protected areas on state-owned land. The rank priority maps and the list of candidate expansion sites was used in Metsähallitus as part of an internal decision-making process together with inventory data from Finnish environmental non-governmental organizations and expert-views from within Metsähallitus. We did not do formal validation on the result obtained in Chapter **I**, but qualitative feedback from experts in Metsähallitus confirmed that most sites suggested were indeed of high conservation value (Panu Kuokkanen, pers. comm.).

In addition to providing informative decision-support tool for implementation of an on-the-ground conservation programme (METSO), we also demonstrated how to successfully use forest inventory data in combination with a spatial prioritization tool – Zonation – to analyze a large spatial extent at a resolution relevant to management decisions (**I**). Conservation planning analyses with similar aims have been done before over the same extent and using partly the same forest inventory data (Juutinen et al. 2008; Kallio et al. 2008; Luque & Vainikainen 2008). Yet to my knowledge, our approach was the first to employ a broad-scale complementarity-based (see 1.1) prioritization method also accounting for several types of connectivity.

Quantitative spatial conservation prioritization can thus be informative at spatial scales ranging from regional (**IV**) to national (**I**, **III**), and for single species (**III**) or multiple forest types (**I**, **IV**). Could we combine similar prioritizations into a single analysis to create a more complex model that accounts for more factors simultaneously? For example, by combining the models of conservation value used in Chapters **I** and **III,** we could create a prioritization that would nominally account for the objectives of both the METSO-programme and capercaillie conservation. However, given the different models of conservation values in the chapters we would face trade-offs in the prioritization process. Zonation produces a well-balanced solution, which might not be a very good solution for the individual objectives, unless the objectives were complementary. Consequently, the results could be hard to interpret and would have reduced utility for the decision-making process. This point is a particularly important to consider when working with practitioners and stakeholders to whom including as many factors into a single analysis may seem like a desirable option: interpreting the results becomes difficult.

While the prioritization analyses based on forest inventory data do produce informative results, we need more data directly relevant for biodiversity (Lindenmayer & Likens 2010). For example, in boreal forests dead wood in is a key resource on which many threatened species depend on (Martikainen et al. 2000; Siitonen et al. 2000; Siitonen 2001; Stokland et al. 2012). While some forest planning and management organizations inventory the occurrence of dead wood, no comprehensive data are available over broad extents. Broad-scale forest inventories are ever-evolving systems and lessons learned from spatial conservation prioritization could also be used to target data collection efforts.

To conclude, habitat quality indices combining quantitative forest inventory data and expert knowledge can be used as inputs in Zonation to produce informative conservation priorities. The utility of the results depends on the details of the objective and the ecologically based model of conservation value that underlies analysis.

4.2 DATA SHOULD HAVE HIGH ENOUGH SPATIAL RESOLUTION AND DETAIL

The resolution of the input data affects the spatial patterns of conservation priority (**II**). The spatial overlap and correlation of priorities between rankings at different spatial resolutions is surprisingly low (**II**). For the best 10% of the landscape, the spatial overlap between two high-resolution (100 and 200 m) solutions was only 0.5 as measured by the Jaccard's index (Figure 6A), or 0.7 as measure by Kendall's Tau rank correlation (Figure 6B). Calculating the spatial overlap and the rank correlation between high- (100 m) and a low-resolution (25 600 m) solutions yielded values of approximately 0.2 and 0.3, respectively. Furthermore, the level of biodiversity feature representation was higher at high-resolution solutions (Figure 5 in **II**). In other words, we need to protect a smaller fraction of the landscape to achieve the same well-balanced combination of biodiversity features when using high-resolution analysis. Alternatively, we can protect higher levels of features with the same fraction of the landscape protected if we use high-resolution data. This result arises from the fact that in the forest mosaic landscape of Finland, large grid cells only include a small fraction of top-quality habitat.

The type of forest inventory data used affects the level of detail of the prioritization. We found out that a spatial conservation prioritization based only on the MS-NFI data and Zonation can produce informative results over broader spatial extents (**IV**). Validation of the results (see 4.1 and **IV**) revealed that protected areas received higher than median (~0.71) priorities in analysis that used only the MS-NFI data (Figure 5). Protected areas in the region are large enough that their aggregate structural features are correctly represented in the coarser MS-NFI data. However, the analysis was unable to account for narrow-distribution forest types and thus lacks the precision found in more detailed forest inventory data (**IV**). Woodland key-habitats, which are smaller than protected areas, received a median rank of ~0.48 which means that the analysis could not distinguish them from the rest of the landscape when using MS-NFI data.

Using incomplete data runs the risk of commission (we prioritize a site based on feature that does not in reality occur there) and omission (site not prioritized because a feature is mistakenly thought to be absent) errors (Rondinini et al. 2006). How much do we risk if we use coarser data instead of more detailed data in prioritization? We analyzed the replacement cost (Cabeza & Moilanen 2006; Moilanen et al. 2009a) of using coarser forest inventory data (i.e. the MS-NFI data) and found out that the cost can be great (Figure 5 in **IV**). Protecting the best 10% of the landscape using the rank priority map from the analysis with the more detailed data covers on average ~54% of the distribution of biodiversity features, while the analysis based on the MS-NFI data covers on average only ~16% of the distribution of biodiversity features. We also examined how robust

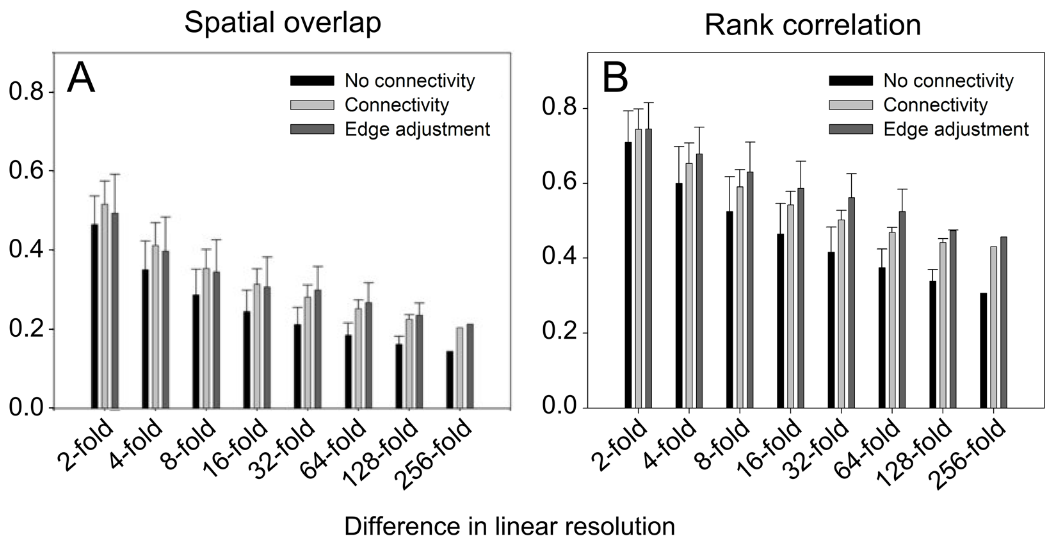

Figure 6. A: Mean spatial overlap (Jaccard similarities) and standard deviations between the best 10% of Zonation prioritization solutions in different spatial resolutions. **B**: Kendall's Tau rank correlations between Zonation rankings of areas prioritized for conservation at different spatial resolutions. The solutions within each analysis type (no connectivity of cells, connectivity of cells, and edge adjustment; see Chapter **II**) were compared with all other resolutions within the same analysis type. Bar graphs show increasing discrepancy in the spatial resolution of data decreases both the spatial overlap of top-priorities as well as the overall correlation between the solutions.

the most informative parts of the prioritization are to differences in data resolution and detail. Usually the highest or lowest priorities are of interest to us. For example, we might be looking for the best places for new protected areas, or we could be targeting intensive forest management operation to areas where they have the least impact on biodiversity. The location of the highest and the lowest priorities are more robust to the data resolution (**II**) and detail (**IV**) than the intermediate priorities, but there is much variation. After 2-fold increase in the data resolution, the spatial overlap of the best 10% of the landscape was on average 0.5 (Jaccard's index, **II**). The spatial overlap of the best 10% of the landscape between analyses based on the coarser and the more detailed data was also approximately 0.5 (**IV**).

Collectively, the results I have presented in this subsection have important ramifications for spatial conservation prioritization. First, spatial conservation prioritization is best done at a spatial extent and resolution relevant for the underlying ecological processes and the planning context at hand. Some authors have suggested a two-stage approach, where a coarse-resolution prioritization is done first, followed by a high-resolution prioritization targeting the top-priorities identified by the coarse-resolution prioritization (Larsen & Rahbek 2003). According to our results, this might not be a sound strategy. Second, a high-resolution analysis – if computationally feasible – can be more cost-efficient if planning units used are also are of high resolution. High-resolution data and high-resolution planning units (pixels, or e.g. forest stands) enable high accuracy in selecting areas that have the highest occurrence of features (i.e. there is only little redundancy). However, very small or poorly connected areas may not be able to sustain viable populations of forest species (Warman et al. 2004; Moilanen & Wintle 2007). Therefore, high resolution alone is not enough, but combined with computational methods that can account for spatial interactions (such as connectivity) cost-efficient solutions are possible. Third and finally, our results provide arguments for using as detailed data as possible when available. Not all forest inventory data is freely available (**IV**). Although it is generally possible to gain access to the data for research purposes, doing so requires investing resources (i.e. time and possibly money) and therefore merits careful consideration in operative conservation planning.

To conclude, the spatial resolution of input data should closely match to those of the planning objectives and the ecological processes involved. Using high-resolution data when available and computationally feasible is recommendable, but is alone not sufficient for guaranteeing species persistence; conservation actions should target areas that are sufficiently large, good quality, and well connected. The level of detail in the forest inventory data used defines how well the prioritization is able to identify small, but valuable forest types and habitats. For broad, regional-scale prioritization coarse inventory data works as well, but for local-scale operative planning detailed data are needed.

4.3 CONNECTIVITY IS IMPORTANT FOR THE RESERVE NETWORK, BUT CAN ENTAIL TRADE-OFFS

Including connectivity increased the spatial aggregation of priorities especially over broader spatial extents (**I**-**IV**). This aggregation decreased the effects that spatial resolution (**II**) and data detail (**IV**) have on the prioritization results. In other words, the results of prioritizations become more correlated and have more spatial overlap among the top-priorities when connectivity is accounted for. Accounting for connectivity between different forest types does not decrease feature representation (**II**, **IV**). That is, accounting for connectivity between forest types does not lead to substantial performance-loss in terms of representation.

We observed an explicit relationship between connectivity and the spatial resolution of the data used in the prioritization. Regardless of the connectivity method used in Zonation (3.5.2), we must define an ecologically justified spatial scale over which connectivity is relevant. Typically, this scale is derived from the dispersal and movement capabilities of a particular species (as the capercaillie in **III**), or in case of several species, from reasonable estimates of the average dispersal capabilities. Also, the typical home range size of a species can be converted into a spatial scale (**III**). If the spatial scale used is small in relation to the spatial resolution of the data, then

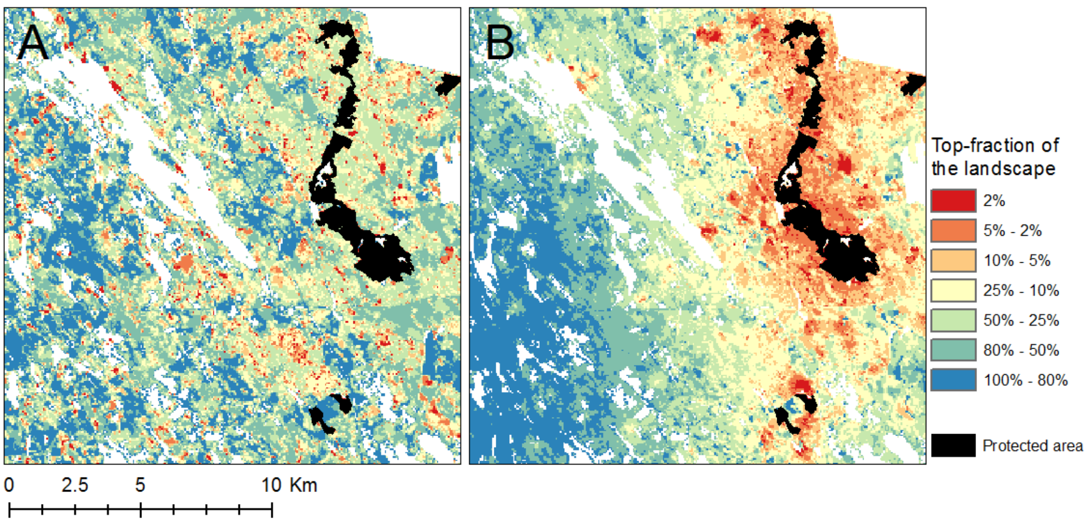

Figure 7. The zero-sum game of spatial conservation prioritization. Colors in the maps correspond to particular hierarchical priority ranks, i.e. red is the best 2% of the landscape etc. Panel **A** shows a non-spatial solution, in which no connectivity methods have been used. In other words, it accounts only for the weights of features and feature representation levels in each cell. Panel **B** shows the effects of multiple connectivity methods simultaneously. The shift in priority patterns is caused by a positive connectivity interaction that emphasizes proximity to protected areas, which are shown in black. Here, connectivity increases the priorities of forest areas near the protected areas. Increased priorities near the protected areas are compensated by reduced priorities further away, even if the quality of the sites is high.

the effects of connectivity will be very small and localized (**II**, **IV**), significantly distorted or even lost. Furthermore, the benefits of high-resolution analysis (4.2) are reduced when the connectivity effects are dominant (**II**).

There is an inherent and almost inevitable trade-off between connectivity and local quality. Here, local habitat quality means the aggregate representation levels of all of the biodiversity features occurring in a given pixel. Applying a connectivity transformation on the biodiversity features in Zonation means regions with relatively high densities of high-quality pixels will be assigned elevated priorities. In contrast, isolated high-quality pixels will lose relative value (Moilanen et al. 2005; Figure 7). This trade-off between increased connectivity and increased protection of high-quality existing areas is an important consideration whenever connectivity is promoted as a conservation strategy (Hodgson et al. 2009, 2010). A further consideration is to define how much and what types of connectivity are needed in spatial conservation prioritization (Moilanen et al. 2009c; Hodgson et al. 2010). This is not an easy task due to species-specific character of connectivity and the multitude of connectivity metrics found in scientific literature.

Areas close to different types of edges can sometimes have reduced priorities for technical reasons. If part of a pixel contains e.g. water, its connectivity value is smaller than that of another cell with full coverage of the same features. Connectivity will also be lower if adjacent cells do not contain biotic or abiotic prerequisites for the features in question. Connectivity values can thus decrease toward, for example, lakeshores or toward country borders, borders, beyond which data are not available. In reality, these areas might contain high-quality habitat. To account for this, we introduced a novel technical feature, "edge adjustment", in Zonation (**II**).

We showed including connectivity in the prioritization improves the results for specific planning objectives. In Chapter **III**, we included connectivity at several different levels. Using the matrix-connectivity method in Zonation (3.5.2), we accounted for connectivity at both the home-range scale and the population scale of the capercaillie. In addition, we emphasized structural forest heterogeneity and included negative connectivity interaction (see 3.5.1) to human-impacted areas, which the capercaillie is known to avoid. Including these four connectivity components in the analysis enabled us to locate continuous and less-disturbed forest areas potentially suitable as capercaillie lekking-landscapes. The improvement of the results was evident when we validated the results against the known lekking-sites of the capercaillie (Figure 5 in **III**).

In addition to ecological justifications, connectivity can also be desirable for the logistics of establishing and maintaining conservation areas (Moilanen et al. 2009c). In chapter **I**, we addressed two logistic constraints with connectivity. First, the potential reserve expansion sites had to be compact enough and of a certain size (approximately 36-100 ha, see **I**) to facilitate implementation. Second, the potential sites also had to be relatively close to existing protected areas again for logistic reasons. Note that the proximity to existing protected areas is justifiable also from the ecological perspective. Protected area networks should be able to support the persistence of species over time (Cabeza & Moilanen 2001; Gaston et al. 2006), and species' ability to disperse between and from individual protected areas is therefore important.

To conclude, accounting for connectivity aggregates priorities spatially and has two justifications: ecological and logistic. Promoting ecological connectivity enhances the persistence of species in the landscape, but cannot substitute for habitat area and quality. Logistically, considering the spatial configuration of conservation action can often reduce per-unit expenses, thereby promoting cost-efficiency. Strongly promoting connectivity can increase the priority of well-connected medium-quality sites at the expense of isolated high-quality sites.

4.4 SPATIAL FOREST CONSERVATION PLANNING SHOULD BE INTEGRATED WITH GENERAL FORESTRY PLANNING

In Southern Finland, more than 95% of forests are under commercial management (Virkkala & Rajasärkkä 2006; Finnish Forest Research Institute 2013). There is very little potential to protect natural or natural-like forests (Kuuluvainen & Aakala 2011; Hanski 2011) so conservation action must span the whole landscape including commercially managed forest. The road to effective forest conservation is therefore a combination of different conservation strategies and actions including setting aside valuable sites, maintaining and restoring valuable forest habitats, and promoting sustainable forest management practices (Lindenmayer et al. 2006; Hanski 2011; Kuuluvainen & Grenfell 2012; Halme et al. 2013; see also Box 2). Organizations practicing forest planning and management are in a key role for several reasons. First, organizations such as Metsähallitus or the Finnish Forest Center either directly manage or oversee management in all public and a large fraction of private forests in Finland. These organizations and professionals working for the organization make concrete decisions about biodiversity conservation (Primmer 2011). Second, these organizations employ experts whose participation in spatial conservation prioritization projects in invaluable (4.5). Third, the organizations have in place operational planning systems that can both provide information (such as up-to-date forest inventory data) for and use the information from spatial conservation prioritization.

What might broad-scale conservation planning look like in landscapes managed predominantly for wood production? Hanski (2011) proposed an approach, in which a third of the whole landscape is managed as multi-use conservation landscape, within which a third is completely protected. Management within conservation landscapes would be less intensive and geared towards favoring structures important for biodiversity instead of trying to maximize wood production. Management instruments such as prolonged rotation times (Koskela et al. 2007) green-tree retention (Gustafsson et al. 2010), prescribed burning (Berglund et al. 2011), and uneven-aged forest management (Kuuluvainen et al. 2012) could be used. The best combination and the spatial allocation of management activities would call for spatial planning and prioritization. Together with the core of protected areas, conservation landscapes would promote the persistence of biodiversity on larger areas (one third of the landscape) than currently. The other two-thirds of landscapes would remain under intensive forest management with lowered environmental regulation. Essentially, biodiversity conservation efforts would be more concentrated than in the current model in which they are spread thinly over the whole landscape.

We showed that there is only limited potential for protecting herb-rich forests – the most species rich forest habitat in Finland – on public land (**I** and 4.1). We also found out that given our ecologically based model of conservation value, the current protected area network does not represent well the more fertile forests with relatively large proportions of deciduous trees. Our conclusions do not mean that there are no priorities on state-owned land or that the protected area network would be ineffective in all possible terms. State-owned forests include a lot of mature heath-forests with potentially high amounts of dead wood and valuable peatlands (Finnish Forest Research Institute 2013). However, these features were not primary targets of our approach. Protected area networks are rarely comprehensive, representative, and adequate for all elements of biodiversity (Margules & Pressey 2000; Scott et al. 2001; Lindenmayer et al. 2006). Nevertheless, the existing protected areas should be complemented accounting for the occurrence of biodiversity on public and private land at the same time.

Expanding the protected area network especially in Southern Finland cannot be restricted to public land; we must find ways to protect valuable forest site also on private land. Since its initiation, the METSO-programme has provided conservation instruments for protecting privately-owned forests based on voluntary action by forest owners (Box 2; Finnish Government 2008). Landowners generally accept voluntary protection measures better than compulsory land acquisition because it retains the freedom of choice with the individual landowner (Segerson & Miceli 1998; Primmer et al. 2014).

Voluntariness does pose challenges to spatial conservation prioritization. Most notably, we can prioritize areas for a particular action (such as protection), but the implementation of the action depends on the willingness of the landowner to participate (Knight et al. 2011a). This, in turn, may compromise the complementarity of the planning. Furthermore, connectivity is not so easy to achieve when spatial decisions depend on voluntary participation. Nevertheless, spatial prioritization analyses can still be informative for the authorities. The approach we present in Chapter **IV** is being used (see 3.2) in the METSO-programme to inform professionals in two ways. First, while what can be protected in METSO depends on what the landowners offer, often the regional authorities receive more offers than they can actually approve. In these cases, the prioritization products can provide decision-support especially when connectivity needs to be accounted for. Second, not all landowners are aware of the METSO-programme. In key regions identified by the spatial conservation prioritization analysis, authorities can approach landowners to see if they would be interested in participating.

In Southern Savonia, we worked with the local ELY not only to develop the prioritization approach, but also to build capacity within the organizations. This capacity building has had two components: the technical and the human component. I will address the technical component here and the human component in subsection 4.5.

Ideally, the prioritizations we did should be repeatable; over time the planning situation changes, data are updated, and errors are detected in the prioritization process. Eventually the organizations should have the capability at least to semi-regularly repeat the prioritization process. Many of the phases of the data preparation analysis itself can be quite complex (**V** and Figure 4) and require specialized technical skills in e.g. GIS, data management, and visualization. Unless an organization employs experts adept with these skills, such technical capability requires either consulting external experts or building and deploying automated tools. We have developed and deployed such pre-processing tools (see 3.4) within the Finnish Forest Centre and these tools have since been used by other organizations as well.

To conclude, the protected area network alone cannot guarantee the persistence of Finnish forest biodiversity. The majority of Finnish forests are under commercial management. Spatial conservation planning should account for public and private forests simultaneously. Spatial conservation prioritization methods could inform forest management about which areas should be set aside (taking into account biodiversity feature occurrence and connectivity) or where forest management operations would cause the least harm to biodiversity.

4.5 ENGAGING EXPERTS IS REQUIRED IN QUANTITATIVE SPATIAL CONSERVATION PRIORITIZATION

Experts (see 3.5.2) have had an important role in many of the chapters of this thesis. In fact, it would not have been possible to carry out the spatial conservation prioritizations without input from experts. Given that decisions related to the management objectives and potential management actions are inherently subjective (Martin et al. 2009), there is always a reasonable amount of expert and stakeholder participation in spatial conservation prioritization (Knight et al. 2006a; Ferrier & Wintle 2009). I initially engaged with experts expecting to learn the relevant information (such as what are the available data and how should we weight biodiversity features, **I**). In their typology for model of knowledge capture, Lynam et al. (2007) call this model "extractive use" in which knowledge, values, or preferences are synthesized by the extracting, group which then passes them on to decision-making process. However, instead of one-directional information extraction, bi-directional information exchange describes better my experience of expert-engagement. Information exchange with experts in my case turned into what Lynam et al. (2007) called "co-learning" in which new information is synthesized jointly and then passed into a decision-making process.

Investing the time and effort to engage with the experts is important for at least two reasons. First, by helping the experts to understand what kind of information they are expected to provide, they are more willing to participate and more likely to provide reliable information (McBride & Burgman 2012). Second, the experts involved may partly be the same managers and practitioners who are supposed to be informed by the prioritization, or they represent organizations responsible for conservation implementation. Involving such participants can not only greatly enhance the successful uptake of the information provided by the prioritization, but also teach scientists to provide right knowledge in the right context (Knight et al. 2006a; Opdam 2010). For example, the pathway from the raw forest inventory data into the habitat quality indices used in Chapter **IV** is complex and would have not been possible to implement without close involvement of experts from the Finnish Forest Centre. Having been involved in the processing steps made it easier for the experts to understand the results of the prioritization and integrate with the rest of their operative information systems. Co-learning and knowledge transfer are key elements in capacity building within any organization (Figure 8). One important lesson to be learned is that there never is a single, true result. It is easier to understand to strengths and weakness of an approach when actively participating in the whole process.

However, relying on expert knowledge is not without risks and limitations. By definition, experts have experience and intricate knowledge in their particular field of expertise. Outside their field of expertise they do not necessarily have any more information on a given topic than anyone else, and the exact context where one's expertise applies may be hard to determine (McBride & Burgman 2012). Experts also regularly have over-confidence in their own knowledge (Speirs-Bridge et al. 2010) and may exhibit different and personal motivational biases (Martin et al. 2012). Formal elicitation techniques can be used to mitigate the effects of various biases (Arnott 2006; McBride & Burgman 2012), but in my thesis I have not used such techniques. Therefore, the accuracy of the expert knowledge I have used remains unknown. However, we did test the sensitivity of the results to particular expert-knowledge based values. For example, in Chapters **II** and **IV** we tested several different connectivity scales and found that the results were not very sensitive to an exact distance measure used. In Chapter **III**, we also tested several different weighting schemes for the biodiversity features used. We concluded that within a reasonable range of weights, the effect of varying weights was quite small (see also Chapter **V** for discussion on how to set weights in the first place). In future, using quantitative expert-elicitation techniques (e.g. Runge et al. 2011; McBride & Burgman 2012; Martin et al. 2012; Price et al. 2012) would enhance our approach.

Figure 8. Experts from the FFC (Marko Keisala on the left) and Metsähallitus NHS (Ninni Mikkonen on the right) examining priority maps in the field. Field-visits are necessary for groundtruthing Zonation results and provide an environment for co-learning (see text).

During my research it was clearly demonstrated that the different experts I have been working with (including some decision-makers) have generally been receptive to the idea of spatial conservation prioritization and using a computational tool such as Zonation. After an initial introductory phase, experts have usually quite quickly grasped the benefits of a broad-scale systematic approach to spatial conservation planning that complements the local-level knowledge that the experts have. In fact, after demonstrating the benefits of such an approach – and Zonation in particular – many experts and organizations have expressed an interest in many other applications. Yet, it is important to understand that successfully executing a full conservation prioritization process (using Zonation or some other tool) is much more than just using a computer program. We estimate that in a typical case (Chapter **V**, Table 1) as much as 80% of the total human resources and time are spent acquisition and preparation of the data. Constructing the ecological model of conservation values is typically the next time-consuming phase, and the technical stage of computational analysis usually constitutes to only about 10-20% of the total required time and resources. Often the level of involvement required from the experts may come as a surprise (see also discussion in 4.6).

To conclude, the paucity of available data means that many inputs to spatial conservation prioritization are based on expert-knowledge. Furthermore, implementation-oriented prioritization cannot be done without the participation of experts and other stakeholders. Investing time and effort into working with experts can result in better quality of information and increase the uptake of the results.

4.6 OPERATIONALIZING SPATIAL CONSERVATION PRIORITIZATION REQUIRES A PROCESS MODEL

Operational, implementation-oriented spatial conservation prioritization is typically an iterative process (Figure 4 and **V**). The process can accommodate new data and constraints as they come along and sometimes even the objectives and decision-makers can change. Some parts of the process might have to be repeated more often than others; data pre- and post-processing repeats frequently whereas the recommendations for conservation action are given perhaps once per process iteration. Depending on the specific objectives, data availability, personnel's technical capabilities, stakeholder involvement, and decision-making needs the whole process may be fast to implement or it can take many years to reach the end of the first iteration. As I have discussed in subsections 4.4 and 4.5, there are benefits to the process even before the final planning products are finished. For example, social co-learning helps to better understand the problems and look for potential solutions (Knight et al. 2006b). Problem identification can also help to focus data collection in case no suitable data exist or resources available for monitoring are scarce.

Once the actual spatial prioritization has been done, the results need to be transferred into the decision-making process in some meaningful way. The technical raw outputs of tools like Zonation (such as the rank priority maps and performance curves) are rarely specific enough and informative to implementers as such. Interpretation and redesign of the outputs are usually required to create planning products that are more informative to implementers (Pierce et al. 2005; e.g. Knight et al. 2006a). Based on the experience gained during my research, it seems that the priority maps produced by Zonation are quite easy to understand for most observers without additional post-processing or preparation. However, maps are inherently forms of communication that often carry many intentional and unintentional meanings (Tversky 2000).

In the case of rank priority maps produced by Zonation, it is extremely difficult to convey all the necessary information on what exactly produced the priority map (i.e. the components and the structure of the ecologically based model for conservation value, the data, and the operating principles of Zonation). For example, most people examining a rank priority map will eventually ask the question why the priority patterns are the way they are. Why is that site high priority? Why is some other site low priority? Rather than presenting the rank priority maps alone, it is often useful to combine them with the original or auxiliary data. Furthermore, the post-processing options that Zonation has may help to summarize the original data and to produce informative aggregate statistics over particular planning units (e.g. the Landscape Identification feature).

Before committing into a spatial conservation prioritization process, it is worth considering the benefits, disadvantages, and threats involved. The content of each of these categories will depend on which type of stakeholder is in question (e.g. scientist, administrator, landowner etc.), but commonly shared considerations include time and money invested, information gained, and the risks of failure (for a longer listing, see Appendix Table A1 in Chapter **V**). In most cases planning and executing a spatial conservation prioritization process will be a significant investment in time and effort. Nevertheless, once the groundwork has been laid, iterating the process will be quicker and easier. Sometimes it can also happen that we simply do not have the necessary data available in which case quantitative spatial conservation prioritization tools cannot be used.

From a broader decision-making context, the advantages of spatial conservation prioritization are also related to the effectiveness of knowledge transfer between the prioritization and decision-making processes. Cash et al. (2003) propose that there are three factors to scientific knowledge that affect its uptake: credibility, salience, and legitimacy. Credibility refers to the scientific accuracy and strength of evidence gathered. Salience measures how useful the knowledge produced is in the particular decision-making context, and legitimacy reflects how well the knowledge recognizes the various interests and values of stakeholders involved. Scientists seem to be mostly preoccupied with credibility, while for decision-makers and stakeholders salience and legitimacy may be more pressing concerns (Cash et al. 2003; Opdam 2010).

There are several factors important to conservation prioritization, such as social and political factors (Knight et al. 2011b), which I have omitted in this thesis. Perhaps the most glaring omission is costs of conservation (Naidoo et al. 2006; Pressey et al. 2007; Nelson et al. 2009). While accounting for costs is undeniably important in many conservation decision-making contexts, they have been less so for the chapters of my thesis. For example, in Chapter **I** the objective of the prioritization was to find the most suitable reserve expansion sites on state-owned land. Implementation of the plan meant that some commercially managed forest sites would be set aside, but within areas governed by the state. In other words, there were no direct acquisition costs to be considered. There were, however, opportunity costs for the state. Areas permanently set aside cannot be used for wood production which means lost revenues for the state. We could have included the opportunity costs in the analysis, but Metsähallitus Natural Heritage Services (the state authority) requested biodiversity-oriented analysis without regard to costs.

So far, costs have not been considered in the prioritization done for the METSO-programme either. The results are to be used for two different purposes: to prioritize between offers by landowners and to identify key regions where landowners should be approached. Both of these objectives clearly have a cost-component. For cost-effective use of public funding, authorities should be striving to prioritize cheaper offers (ecological values being equal) and METSO-promotion could be targeted in areas where the compensations would be low.

Finally, while I have specifically addressed implementation related issues here, not all spatial conservation prioritization aims at implementation. There is a significant amount of scientific work being done that studies the theoretical, conceptual, and computational aspects of spatial conservation planning without expecting a direct link to implementation.

To conclude, spatial conservation prioritization is an iterative process that can require significant time and human-resource investments. Before considering operative use, individuals and organizations should assess what the process would look like. Establishing a conceptual model for the process can help to estimate the costs and benefits involved, to formulate the right questions, and to select the most suitable tools.

4.7 SHARING DATA AND ANALYSIS IMPLEMENTATION CAN IMPROVE RESULTS AND INCREASE RE-USE

Data availability can seriously restrict the breadth and depth of analyses we can do (**II**, **IV**). On the other hand, making the research products openly available has facilitated their uptake amongst the practitioners (**III**). Nevertheless, data availability has several dimensions. Suitable data have to exist in the first place so that we can use it in spatial conservation prioritization. For the majority of features we would like to include in our analysis, we simply do not have the data. Then, if suitable data exists in principle, they have to be available at the extent and resolution that is relevant both ecologically and for the planning need at hand. Even when data is apparently available, further investigation may reveal that it is biased, outdated, otherwise of dubious quality, or in a format that is very difficult to access efficiently.

The third, and thus far unmentioned dimension, is the level to which the data is accessible in any practical terms. The relevant data might exist, but access to it may be restricted due to proprietary rights or usage fees. This applies both to research data as well as large datasets collected and maintained by public and private forestry organizations. Open access to data is especially desirable from the decision-making point of view because of the many benefits it entails, such as enabling integrative and synthesizing science (Carpenter et al. 2009), enabling exploration of new topics not envisioned by the data originators (Uhlir & Schröder 2007), and providing more verifiable research for policymakers (Wolkovich et al. 2012). One of the advantages attributed to systematic conservation planning and spatial conservation prioritization is the transparency of the process that follows from the explicit definition of high and low level objectives and the formal quantitative methods used (Margules & Pressey 2000; Bekessy et al. 2012). Making the data openly available would seem like the best way to achieve transparency, accountability, and repeatability of the analyses that support decision-making.

Metla opened up the MS-NFI data in 2013 (http://www.metla.fi/ohjelma/vmi/vmi-moni-en.htm), which means that all the necessary input data (but not the validation data), pre-processing scripts, Zonation setups, and the result associated with Chapter II can be openly shared. At the time of writing, the process publishing all the components mentioned is in progress. All the setups that we used in Chapter IV are available in GitHub online repository (https://github.com/jlehtoma/zsetup-esmk) under a permissive license (CC-BY SA 3.0). As the version in a version control system may evolve over time, the version 1.0 used at the time of writing is available also in figshare (Lehtomäki 2014). The whole prioritization analysis is not, unfortunately, repeatable because all input data cannot be shared for legal reasons.

Continuing the operationalization of the spatial conservation planning tools requires that we make methods and workflows transparent and repeatable. Conservation prioritization processes involve several stages (Figure 4) that are both technical and error-prone. Making the implementation of the whole computational process openly available increases the transparency and thus also the legitimacy of the whole approach. While it is true that the exact parameter values used will ever be of interest only to a relatively small technically-inclined group of people, they do nevertheless exactly document what was done. "What" is of little use without answers to a corresponding "why", and therefore appropriate documentation of the decisions taken should accompany the final planning products. Following particular conventions, best-practices, and documenting the computational workflow helps. Importantly, sharing the technical implementation – not just the final products – means that the analyses are re-usable and adaptable (Ram 2013). This is particularly important in conservation to bridge the gap between scientific literature and practitioners. In case of Zonation setups, making them publicly and openly available is a first step towards a library of setups that can cover a variety of planning needs.

To conclude, making use of the best possible information in conservation decision-making requires access to that information in the first place. Open access to relevant data also improves the quality of decision-support tools. Sharing the products of spatial conservation prioritization increases their uptake. Sharing the technical implementation of the methods and workflows used is equally important to open data access.

5 CONCLUDING REMARKS

This thesis specifically deals with spatial conservation prioritization for Finnish forest conservation management. The results concerning the effects of spatial resolution, detail, and connectivity are dependent on the data and method (Zonation) used, but I would expect that many of the conclusions can be generalized.

The forest inventory data we have used varies relatively smoothly across the landscape when compared to other types of data frequently used in spatial conservation prioritization (such as species occurrence data). For data with more abrupt occurrence patterns and higher features richness, the effects of data resolution and connectivity would probably be greater. Many countries over the world have similar kinds of National Forest Inventory systems in place as Finland (Tomppo 2006b; Chirici et al. 2011), which implies that the approaches

I have presented here could be applied in other countries with similar prioritization needs. In fact, the tools I have developed as part of my work (see 3.4) specifically aim to facilitate the uptake of the prioritization approach elsewhere. There is nothing particularly country-specific in working with the experts (see 4.5) or about the structure of the prioritization process (see 4.6). However, both will always require case-specific consideration regardless of the country at hand.

The extent to which my results are specific to Zonation is somewhat hard to measure, because no other software implementation operates on the exactly same principles. Other popular conservation planning software such as Marxan (Possingham et al. 2000), Marxan with Zones (Watts et al. 2009) and ConsNet (Ciarleglio et al. 2009) all operate based on the concepts of target-setting and stochastic optimization. Furthermore, these software handle e.g. connectivity, uncertainty, and administrative division of the landscape in very different ways (see Chapter V for more thorough comparison). I stress that Zonation is not the only tool available, and each tool is designed to tackle a particular problem, and the most suitable tool depends on the prioritization context and objectives. As always, the appropriateness of a particular tool should be considered case-by-case.

The wealth of approaches and software available for spatial conservation prioritization does not mean that there is no more important research to be done, quite the contrary. Based on my own work, further research is needed on the effects of using quantitatively and qualitatively heterogeneous data in conservation prioritization analyses. For example, issues related to scale (e.g. the effects of aggregating data (Fisher 1997)) remain relatively poorly studied in spatial conservation prioritization literature. Prioritizations are only as good as the data that they are based on. This is especially the case in my own work, in which I have used relatively simplistic conservation value indices based on structural forest features. Ecological studies in establishing empirical links between species and forest structures are clearly a research priority as well. Finally, chapters I-IV in this thesis provide prioritization solutions that offer insights and may be useful in practice, but that are inherently static in space and time. Finnish forest landscapes are, however, very dynamic because natural succession, forest management, and the changing climate. Moreover, the solutions concentrate on a single conservation action at a time. In this thesis, I have advocated integrating spatial conservation prioritization into general forest management. Methodologically, this means that we need to be able to account for deploying multiple actions at the same and for landscape-level dynamics. Fortunately research into these topics is already well under way (e.g. Mönkkönen et al. 2011, 2014; Leroux & Rayfield 2013; Mazziotta et al. 2013)

At the time of writing this thesis, quantitative spatial conservation planning is being increasingly used in different conservation projects and implementation in Finland (see Table 1 in 3.2), including the METSO-programme. From practical point of view, our technical capability in using quantitative analysis tools is quite good, there is room for improvement in incorporating these tools in the wider conservation planning process. Working together with decision-makers and practitioners, we need to direct more attention to developing precise and realistic low-level objectives that can be used in the actual prioritization. Furthermore, we need to be able to wrap the results of spatial conservation prioritization into planning products that practitioners can use. Ultimately, insights gained from the technical assessment phase of conservation prioritization should also feed back to the decision-making process.

Currently the METSO-programme is among the biggest investments that the Finnish government is allocating to environmental and biodiversity conservation. In summer of 2014, the decision was reached that the programme will be continued until 2025 (Finnish Government 2014). The wide acceptance of the programme among landowners has probably improved the reception of biodiversity conservation in general. Yet, even if the conservation targets of METSO (~100 000 ha on private land and ~25 000 ha on public land) would be met in full, in absolute terms the increase would be modest (the total forest land area in Finland is ~22.8 million ha (Finnish Forest Research Institute 2013)). This has several implications. First, since the METSO is a significant public investment, its efforts should be allocated in the best way possible. Spatial conservation prioritization can help to achieve this.

Second, since the overall area targets of METSO are modest at best, implementation of METSO should be integrated with other conservation instruments used in forest management and general land-use planning. For example, less intensive management regimes could be established in the proximity of METSO sites. Conservation landscapes proposed by Hanski (2011) (see 4.4) is an example of what such an approach could mean conceptually. . In practice, an operational model for conservation planning (Knight et al. 2006b, 2013) needs to be devised with scientific assessments on the effective ways of implementing conservation actions. Spatial conservation prioritization is one key activity in such assessments. Third and finally, we should critically evaluate the targets set in METSO and if needed, revise them. To maximize the potential METSO has, we should put the best available information and tools to practice. Nature knows no borders and ideally, we should account for this in national planning. In Finland, forests close to the Russian border seem to be important for wildlife species richness and abundance in general (Lindén et al. 2000). Largely because of the differences in the forest management histories between the two countries, Russia still has more natural or natural-like forests left close to the Finnish border (Burnett et al. 2003). Accounting for the forest structure and potential source habitats on the Russian side of border would increase the ecological realism of the prioritization done in Finland. The circumpolar boreal forest zone, the taiga, constitute the second largest biome on Earth (Bradshaw et al. 2009) and much of the conservation action in countries in this zone involves forests. Taking a broader perspective to forest conservation planning is therefore necessary nationally and internationally. Some of the approaches I have presented in this thesis could be applicable internationally as well. Held in 2010, the COP 10 Convention on Biological Diversity in Nagoya, Japan established a new strategic plan for conservation of biodiversity and the maintenance on ecosystem services (Normile 2010; Harrop 2011). Among the targets (so called Aichi targets) specified in the strategy, is to increase to coverage of terrestrial protected areas from 10% to 17%. A collaborative effort in the Fennoscandian and Barents region utilizing the best national datasets available and spatial conservation planning methods would make a strong example of what the Nagoya agreement can achieve. To paraphrase Mermet et al. (2013): while there is no unity of aims, no close coincidence of interests, and no consensus on responsibility, at least we have tools for organized joint action. Now we must find the ways to put those tools into practice.

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One broad conclusions of thesis is that "Engaging experts is required in quantitative spatial conservation prioritization". I certainly stand behind this conclusion and while doing so, would like to acknowledge all the experts and stakeholders from numerous organizations for having participated in the planning processes, workshops, meetings, and training events. You are too many to be named, but are nevertheless a crucial part of making implementation-oriented spatial conservation prioritization count.

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REFERENCES

Arnott, D. (2006) Cognitive biases and decision support systems development: A design science approach. Information Systems Journal, 16, 55–78.

Arponen, A., Heikkinen, R.K., Paloniemi, R., Pöyry, J., Similä, J. & Kuussaari, M. (2013) Improving conservation planning for semi-natural grasslands: Integrating connectivity into agri-environment schemes. Biological Conservation, 160, 234–241.

Arponen, A., Moilanen, A. & Ferrier, S. (2008) A successful community-level strategy for conservation prioritization. Journal of Applied Ecology, 45, 1436–1445.

Barley, S.R. & Kunda, G. (2006) Contracting: A New Form of Professional Practice. Academy of Management Perspectives, 20, 45–66.

Baskent, E.Z. & Keles, S. (2005) Spatial forest planning: A review. Ecological Modelling, 188, 145–173.

Beier, P., Spencer, W., Baldwin, R.F. & McRae, B.H. (2011) Toward Best Practices for Developing Regional Connectivity Maps. Conservation Biology, 25, 879–892.

Bekessy, S.A., White, M.D., Gordon, A., Moilanen, A., McCarthy, M.A. & Wintle, B.A. (2012) Transparent planning for biodiversity and development in the urban fringe. Landscape and Urban Planning, 108, 140–149.

Berglund, H., Önsson, M.T., Penttilä, R. & Vanha-Majamaa, I. (2011) The effects of burning and dead-wood creation on the diversity of pioneer wood-inhabiting fungi in managed boreal spruce forests. Forest Ecology and Management, 261, 1293–1305.

Bettinger, P., Johnson, D.L. & Johnson, K.N. (2003) Spatial forest plan development with ecological and economic goals. Ecological Modelling, 169, 215–236.

Bettinger, P. & Sessions, J. (2003) Spatial forest planning: To adopt, or not to adopt? Journal of Forestry, 101, 24–29.

Bowne, D.R. & Bowers, M.A. (2004) Interpatch movements in spatially structured populations: A literature review. Landscape Ecology, 19, 1–20.

Bradford, J.B. & D'Amato, A.W. (2012) Recognizing trade-offs in multi-objective land management. Frontiers in Ecology and the Environment, 10, 210–216.

Bradshaw, C.J., Warkentin, I.G. & Sodhi, N.S. (2009) Urgent preservation of boreal carbon stocks and biodiversity. Trends in Ecology and Evolution, 24, 541–8.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. Science, 313, 58–61.

Burgman, M., Carr, A., Godden, L., Gregory, R., McBride, M., Flander, L. & Maguire, L. (2011) Redefining expertise and improving ecological judgment. Conservation Letters, 4, 81–87.

Burnett, C., Fall, A., Tomppo, E. & Kalliola, R. (2003) Monitoring Current Status of and Trends in Boreal Forest Land Use in Russian Karelia. Conservation Ecology, 7, 1–29.

Cabeza, M. & Moilanen, A. (2001) Design of reserve networks and the persistence of biodiversity Advances in site-selection algorithms. Trends in Ecology and Evolution, 16, 242–248.

Cabeza, M. & Moilanen, A. (2006) Replacement cost: A practical measure of site value for cost-effective reserve planning. Biological Conservation, 132, 336–342.

Carpenter, S.R., Armbrust, E.V., Arzberger, P.W., Iii, F.S.C., Elser, J.J., Hackett, E.J., Ives, A.R., Kareiva, P.M., Leibold, M.A., Mangel, M., Merchant, N., Murdoch, W.W., Palmer, M.A., Debra, P.C., Pickett, S.T.A., Smith, K.K., Wall, D.H. & Zimmerman, A.S. (2009) Accelerate Synthesis in Ecology and Environmental Sciences. BioScience, 59, 699–701.

Carroll, C., Dunk, J.R. & Moilanen, A. (2010) Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Global Change Biology, 16, 891–904.

Carvalho, S.B., Brito, J.C., Pressey, R.L., Crespo, E. & Possingham, H.P. (2010) Simulating the effects of using different types of species distribution data in reserve selection. Biological Conservation, 143, 426–438.

Cash, D.W., Clark, W.C., Alcock, F., Dickson, N.M., Eckley, N., Guston, D.H., Jäger, J. & Mitchell, R.B. (2003) Knowledge systems for sustainable development. Proceedings of the National Academy of Sciences of the United States of America, 100, 8086–91.

Chirici, G., Mcroberts, R.E., Winter, S., Bertini, R., Bra, U., Asensio, I.A., Bastrup-birk, A., Rondeux, J. & Barsoum, N. (2012) National Forest Inventory Contributions to Forest Biodiversity Monitoring. Forest Science, 58, 257–268.

Chirici, G., Winter, S. & McRoberts, R.E. (2011) National Forest Inventories: Contributions to Forest Biodiversity Assessments. Springer, Dordrecht.

Church, R.L., Murray, A.T. & Barber, K.H. (2000) Forest planning at the tactical level. Annals of Operations Research, 95, 3–18.

Ciarleglio, M., Barnes, J.W. & Sarkar, S. (2009) ConsNet: new software for the selection of conservation area networks with spatial and multi-criteria analyses. Ecography, 32, 205–209.

Corona, P., Chirici, G., Mcroberts, R.E., Winter, S. & Barbati, A. (2011) Contribution of large-scale forest inventories to biodiversity assessment and monitoring. Forest Ecology and Management, 262, 2061–2069.

Cracknell, A.P. (1998) Review article Synergy in remote sensing - what's in a pixel? International Journal of Remote Sensing, 19, 2025–2047.

Di Minin, E. & Moilanen, A. (2013) Improving the surrogacy effectiveness of charismatic megafauna with well-surveyed taxonomic groups and habitat types. Journal of Applied Ecology, 51, 281–287.

Di Minin, E., Veach, V., Lehtomäki, J., Pouzols, F.M. & Moilanen, A. (2014) A Quick Introduction to Zonation. Conservation Biology Informatics Group, Helsinki.

Edman, M., Gustafsson, M., Stenlid, J. & Ericson, L. (2004) Abundance and viability of fungal spores along a forestry gradient - responses to habitat loss and isolation? Oikos, 104, 35–42.

ESRI. (2014) ArcGIS Desktop, Version 10.2.1. Environmental Systems Research Institute, Redlands, CA.

Esseen, P., Ehnström, B., Ericson, L. & Sjöberg, K. (1997) Boreal forests. Ecological Bulletins, 46, 16–47.

Fall, A. & Fall, J. (2001) A domain-specific language for models of landscape dynamics. Ecological Modelling, 141, 1–18.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J. & Macdonald, E. (2014) Can retention forestry help conserve biodiversity ? A meta-analysis. Journal of Applied Ecology, Early view, 1–11.

Ferrier, S. & Wintle, B.A. (2009) Quantitative Approaches to Spatial Conservation Prioritization: Matching the Solution to the Need. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K.A. Wilson & H.P. Possingham), p. 304. Oxford University Press, Oxford.

Finnish Forest Research Institute. (2013) Finnish Statistical Yearbook of Forestry. Metla, Vantaa.

Finnish Government. (2008) Government Resolution on the Forest Biodiversity Programme for Southern Finland 2008-2016 (METSO), http://www.mmm.fi/attachments/metsat/5yckfcmWR/METSOResolution2008-2016_ENGL.pdf

Finnish Government. (2014) Valtioneuvoston periaatepäätös Etelä-Suomen metsien monimuotoisuuden toimintaohjelman jatkamisesta 2014-2025, http://www.ym.fi/download/noname/{E4BA4C28-3815-4E62-87B5-AF9226CF749C}/100323

Fisher, P. (1997) The pixel: A snare and a delusion. International Journal of Remote Sensing, 18, 679–685.

Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., Briers, R. a., Callaghan, C.S.Q., Catchpole, R., Hopkins, J., Kunin, W.E., Latham, J., Opdam, P., Stoneman, R., Stroud, D.A. & Tratt, R. (2006) The ecological effectiveness of protected areas: The United Kingdom. Biological Conservation, 132, 76–87.

GDAL Development Team. (2014) GDAL - Geospatial Data Abstraction Library, Version 1.10.1. Open Source Geospatial Foundation.

Gordon, A., Simondson, D., White, M.D., Moilanen, A. & Bekessy, S.A. (2009) Integrating conservation planning and landuse planning in urban landscapes. Landscape and Urban Planning, 91, 183–194.

Gotway Crawford, C.A. & Young, L.J. (2004) A spatial view of the ecological inference problem. Ecological Inference: New Methodological Strategies (eds G. King, O. Rosen & M.A. Tanner), p. 432. Cambridge University Press, Cambridge.

Grantham, H.S., Pressey, R.L., Wells, J.A. & Beattie, A.J. (2010) Effectiveness of Biodiversity Surrogates for Conservation Planning: Different Measures of Effectiveness Generate a Kaleidoscope of Variation (ed J Moen). PLoS ONE, 5, 1–12.

Gustafsson, L., Kouki, J. & Sverdrup-Thygeson, A. (2010) Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. Scandinavian Journal of Forest Research, 25, 295–308.

Haight, R.G. & Snyder, S.A. (2009) Integer Programming Methods for Reserve Selection and Design. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K.A. Wilson & H.P. Possingham), pp. 43–57. Oxford University Press, Oxford.

Haila, Y. (1994) Preserving ecological diversity in boreal forests: ecological background, research, and management. Annales Zoologici Fennici, 31, 203–207.

Halme, P., Allen, K.A., Auninš, A., Bradshaw, R.H.W., Brumelis, G., Cada, V., Clear, J.L., Eriksson, A., Hannon, G., Hyvärinen, E., Ikauniece, S., Irsenaite, R., Jonsson, B.G., Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T., Mazziotta, A., Mönkkönen, M., Nyholm, K., Oldén, A., Shorohova, E., Strange, N., Toivanen, T., Vanha-majamaa, I., Wallenius, T., Ylisirniö, A. & Zin, E. (2013) Challenges of ecological restoration: Lessons from forests in northern Europe. Biological Conservation, 167, 248–256.

Hannah, L., Rakotosamimanana, B., Ganzhorn, J., Mittermeier, R.A., Olivieri, S., Iyer, L., Rajaobelina, S., Hough, J., Andriamialisoa, F., Bowles, I. & Tilkin, G. (1998) Participatory planning, scientific priorities, and landscape conservation in Madagascar. Environmental Conservation, 25, 30–36.

Hanski, I. (1998) Metapopulation dynamics. Nature, 396, 41–49.

Hanski, I. (2011) Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio, 40, 248–255.

Harrop, S.R. (2011) "Living in Harmony with nature"? Outcomes of the 2010 Nagoya conference of the convention on biological diversity. Journal of Environmental Law, 23, 117–128.

Heikkinen, R.K. (2002) Complementarity and other key criteria in the conservation of herb-rich forests in Finland. Biodiversity and Conservation, 11, 1939–1958.

Heller, N.E. & Zavaleta, E.S. (2008) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation, 142, 14–32.

Hodgson, J.A., Moilanen, A., Wintle, B.A. & Thomas, C.D. (2010) Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology, 48, 148–152.

Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009) Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology, 46, 964–969.

Hokkanen, P.J. (2003) Vascular plant communities in boreal herb-rich forests in Koli, eastern Finland. Annales Botanici Fennici, 40, 153–176.

Horne, P. (2006) Forest owners' acceptance of incentive based policy instruments in forest biodiversity conservation – A Choice Experiment based approach. Silva Fennica, 40, 169–178.

Hujala, T., Pykäläinen, J. & Tikkanen, J. (2007) Decision making among Finnish non-industrial private forest owners: The role of professional opinion and desire to learn. Scandinavian Journal of Forest Research, 22, 454–463.

Jelinski, D.E. & Wu, J. (1996) The modifiable areal unit problem and implications for landscape ecology. Landscape Ecology, 11, 129–140.

Jenkins, C.N. & Joppa, L. (2009) Expansion of the global terrestrial protected area system. Biological Conservation, 142, 2166–2174.

Jonsson, M. & Nordlander, G. (2006) Insect Colonisation of Fruiting Bodies of the Wood-decaying Fungus Fomitopsis pinicola at Different Distances from an Old-growth Forest. Biodiversity and Conservation, 15, 295–309.

Jumppanen, J., Kurttila, M., Pukkala, T. & Uuttera, J. (2003) Spatial harvest scheduling approach for areas involving multiple ownership. Forest Policy and Economics, 5, 27–38.

Juutinen, A., Luque, S., Mönkkönen, M., Vainikainen, N. & Tomppo, E.O. (2008) Cost-effective forest conservation and criteria for potential conservation targets: a Finnish case study. Environmental Science & Policy, 11, 613–626.

Juutinen, A., Mönkkönen, M. & Ylisirniö, A.-L. (2009) Does a voluntary conservation program result in a representative protected area network?The case of Finnish privately owned forests. Ecological Economics, 68, 2974–2984.

Kallio, A.M., Hänninen, R., Vainikainen, N. & Luque, S. (2008) Biodiversity value and the optimal location of forest conservation sites in Southern Finland. Ecological Economics, 67, 232–243.

Kangas, A., Kangas, J. & Kurttila, M. (2008) Decision Support for Forest Management. Springer, Dordrecht.

Kareksela, S., Moilanen, A., Tuominen, S. & Kotiaho, J.S. (2013) Use of Inverse Spatial Conservation Prioritization to Avoid Biological Diversity Loss Outside Protected Areas. Conservation Biology, 27, 1294–1303.

Kindlmann, P. & Burel, F. (2008) Connectivity measures: a review. Landscape Ecology, 23, 879–890.

Klein, C.J., Wilson, K.A., Watts, M.E., Stein, J., Carwardine, J., Mackey, B. & Possingham, H.P. (2009) Spatial conservation prioritization inclusive of wilderness quality: A case study of Australia's biodiversity. Biological Conservation, 142, 1282–1290.

Knight, A.T., Cowling, R.M., Boshoff, A.F., Wilson, S.L. & Pierce, S.M. (2011a) Walking in STEP: Lessons for linking spatial prioritisations to implementation strategies. Biological Conservation, 144, 202–211.

Knight, A.T., Cowling, R.M. & Campbell, B.M. (2006) An Operational Model for Implementing Conservation Action. Conservation Biology, 20, 408–419.

Knight, A.T., Cowling, R.M., Difford, M. & Campbell, B.M. (2010) Mapping Human and Social Dimensions of Conservation Opportunity for the Scheduling of Conservation Action on Private Land. Conservation Biology, 24, 1348–1358.

Knight, A.T., Cowling, R.M., Rouget, M., Balmford, A., Lombard, A.T. & Campbell, B.M. (2008) Knowing but not doing: selecting priority conservation areas and the research-implementation gap. Conservation Biology, 22, 610–617.

Knight, A.T., Driver, A., Cowling, R.M., Maze, K., Desmet, P.G., Lombard, A.T., Rouget, M., Botha, M.A., Boshoff, A.F., Castley, J.G., Goodman, P.S., Mackinnon, K., Pierce, S.M., Sims-Castley, R., Stewart, W.I. & Von Hase, A. (2006) Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. Conservation Biology, 20, 739–750.

Knight, A.T., Rodrigues, A.S.L., Strange, N., Tew, T. & Wilson, K.A. (2013) Designing effective solutions to conservation planning problems. Key Topics in Conservation Biology 2 (eds D.W. Macdonald & K.J. Willis), pp. 362–383. Blackwell-Wiley, Oxford.

Knight, A.T., Sarkar, S., Smith, R.J., Strange, N. & Wilson, K.A. (2011b) Engage the hodgepodge: management factors are essential when prioritizing areas for restoration and conservation action. Diversity and Distributions, 17, 1234–1238.

Kontula, T. & Raunio, A. (2009) New method and criteria for national assessments of threatened habitat types. Biodiversity and Conservation, 18, 3861–3876.

Kool, J.T., Moilanen, A. & Treml, E. a. (2013) Population connectivity: recent advances and new perspectives. Landscape Ecology, 28, 165–185.

Koskela, E., Ollikainen, M. & Pukkala, T. (2007) Biodiversity Conservation in Commercial Boreal Forestry: The Optimal Rotation Age and Retention Tree Volume. Forest Science, 53, 443–452.

Kotilainen, J. & Rytteri, T. (2011) Transformation of forest policy regimes in Finland since the 19th century. Journal of Historical Geography, 37, 429–439.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis Jr, E., Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C., Zjhra, M.L., Philips, S., Dransfeld, J., Jr, L., E., N. & Louis, E. (2008) Aligning Conservation Priorities Across Taxa in Madagascar with High-Resolution Planning Tools. Science, 320, 222–226.

Kukkala, A.S. & Moilanen, A. (2012) Core concepts of spatial prioritisation in systematic conservation planning. Biological Reviews, 88, 443–464.

Kurttila, M. (2001) The spatial structure of forests in the optimization calculations of forest planning - A landscape ecological perspective. Forest Ecology and Management, 142, 129–142.

Kurttila, M. & Pukkala, T. (2003) Combining holding-level economic goals with spatial landscape-level goals in the planning of multiple ownership forestry. Landscape Ecology, 18, 529–541.

Kuuluvainen, T. (2009) Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. Ambio, 38, 309–315.

Kuuluvainen, T. & Aakala, T. (2011) Natural forest dynamics in boreal Fennoscandia: A review and classification. Silva Fennica, 45, 823–841.

Kuuluvainen, T. & Grenfell, R. (2012) Natural disturbance emulation in boreal forest ecosystem management - theories, strategies, and a comparison with conventional even-aged management. Canadian Journal of Forest Research, 1203, 1185–1203.

Kuuluvainen, T., Tahvonen, O. & Aakala, T. (2012) Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio, 41, 720–37.

Larsen, F.W. & Rahbek, C. (2003) Influence of scale on conservation priority setting – a test on African mammals. Biodiversity and Conservation, 2, 599–614.

Larsen, F.W. & Rahbek, C. (2005) The influence of spatial grain size on the suitability of the higher-taxon approach in continental priority-setting. Animal Conservation, 8, 389–396.

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T. & Rodrigues, A.S.L. (2013) Protected Areas and Effective Biodiversity Conservation. Science, 342, 1–3.

Leathwick, J.R., Moilanen, A., Francis, M., Elith, J., Taylor, P., Julian, K., Hastie, T. & Duffy, C. (2008) Novel methods for the design and evaluation of marine protected areas in offshore waters. Conservation Letters, 1, 91–102.

Lehtomäki, J. (2014) Zonation setups for Southern Savonia, http://dx.doi.org/doi:10.6084/m9.figshare.1118842

Leroux, S.J. & Rayfield, B. (2013) Methods and tools for addressing natural disturbance dynamics in conservation planning for wilderness areas (ed M Rouget). Diversity and Distributions, 20, 1–14.

Lindén, H., Danilov, P.I., Gromtsev, A.N., Helle, P., Ivanter, E. V & Kurhinen, J. (2000) Large-scale forest corridors to connect the taiga fauna to Fennoscandia. Wildlife Biology, 6, 179–188.

Lindenmayer, D.B., Franklin, J.F. & Fischer, J. (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation, 1, 433–445.

Lindenmayer, D.B. & Likens, G.E. (2010) The science and application of ecological monitoring. Biological Conservation, 143, 1317–1328.

Lindenmayer, D.B., Margules, C.R. & Botkin, D.B. (2008) Indicators of Biodiversity for Ecologically Sustainable Forest Management. Conservation Biology, 14, 941–950.

Lindstad, B.H. & Solberg, B. (2012) Influences of international forest policy processes on national forest policies in Finland, Norway and Sweden. Scandinavian Journal of Forest Research, 27, 210–220.

Lombard, A.T., Hilton-Taylor, C., Rebelo, A.G., Pressey, R.L. & Cowling, R.M. (1999) Reserve selection in the Succulent Karoo, South Africa: coping with high compositional turnover. Plant Ecology, 142, 35–55.

Luque, S. & Vainikainen, N. (2008) Habitat quality assessment and modelling for forest biodiversity and sustainability. Patterns and Processes in Forest Landscapes (eds R. Lafortezza, G. Sanesi, J. Chen & T.R. Crow), pp. 241–264. Springer, Dordrecht.

Lynam, T., Jong, W. De, Sheil, D., Kusumanto, T. & Evans, K. (2007) A Review of Tools for Incorporating Community Knowledge , Preferences , and Values into Decision Making in Natural Resources Management. Ecology And Society, 12, 5.

Maggini, R., Kujala, H., Taylor, M., Lee, J.R., Possingham, H., Wintle, B. & Fuller, R. (2013) Protecting and Restoring Habitat to Help Australia's Threatened Species Adapt to Climate Change. National Climate Change Adaptation Research Facility, Gold Coast.

Margules, C.R. & Pressey, R.L. (2000) Systematic Conservation Planning. Nature, 405, 243–253.

Margules, C.R. & Sarkar, S. (2007) Systematic Conservation Planning. Cambridge University Press, Cambridge.

Marshalek, E.C., Ramage, B.S. & Potts, M.D. (2014) Integrating harvest scheduling and reserve design to improve biodiversity conservation. Ecological Modelling, 287, 27–35.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation, 94, 199–209.

Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., Mcbride, M. & Mengersen, K. (2012) Eliciting Expert Knowledge in Conservation Science. Conservation Biology, 26, 29–38.

Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C. & Kendall, W.L. (2009) Structured decision making as a conceptual framework to identify thresholds for conservation and management. Ecological Applications, 19, 1079–1090.

Mazziotta, A., Mönkkönen, M., Strandman, H., Routa, J., Tikkanen, O.-P. & Kellomäki, S. (2013) Modeling the effects of climate change and management on the dead wood dynamics in boreal forest plantations. European Journal of Forest Research, 133, 405–421.

McBride, M.F. & Burgman, M.A. (2012) What Is Expert Knowledge, How Is Such Knowledge Gathered, adn How Do We Use It to Address Questions in Landscape Ecology? Expert Knowledge and Its Application in Landscape Ecology (eds A.H. Perera, C.A. Drew & C.J. Johnson), p. 307. Springer, Dordrecht.

Meller, L., Cabeza, M., Pironon, S. & Barbet-, M. (2014) Ensemble distribution models in conservation prioritization: from consensus predictions to consensus reserve networks. Diversity and Distributions, 20, 309–321.

Mermet, L., Homewood, K., Dobson, A. & Billé, R. (2013) Five paradigms of collective action underlying the human dimension of conservation. Key Topics in Conservation Biology 2 (eds D.W. Macdonald & K.J. Willis), pp. 42–58. Wiley-Blackwell, Oxford.

Mikkonen, N. & Moilanen, A. (2013) Identification of top priority areas and management landscapes from a national Natura 2000 network. Environmental Science & Policy, 27, 11–20.

Moilanen, A. (2005) Reserve selection using nonlinear species distribution models. American Naturalist, 165, 695–706.

Moilanen, A. (2008a) Two paths to a suboptimal solution once more about optimality in reserve selection. Biological Conservation, 141, 1919–1923.

Moilanen, A. (2008b) Generalized complementarity and mapping of the concepts of systematic conservation planning. Conservation Biology, 22, 1655–1658.

Moilanen, A. (2012) Spatial Conservation Prioritization in Data-Poor Areas of the World. Natureza & Conservação, 10, 12–19.

Moilanen, A., Anderson, B.J., Eigenbrod, F., Heinemeyer, A., Roy, D.B., Gillings, S., Armsworth, P.R., Gaston, K.J.

& Thomas, C.D. (2011) Balancing alternative land uses in conservation prioritization. Ecological Applications, 21, 1419–1426.

Moilanen, A., Arponen, A., Stokland, J.N. & Cabeza, M. (2009) Assessing replacement cost of conservation areas: How does habitat loss influence priorities? Biological Conservation, 142, 575–585.

Moilanen, A. & Ball, I.R. (2009) Heuristic and Approximate Optimization Methods for Spatial Conservation Prioritization. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K.A. Wilson & H.P. Possingham), pp. 58–69. Oxford University Press, Oxford.

Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B.A. & Thomas, C.D. (2005) Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B: Biological Sciences, 272, 1885–1891.

Moilanen, A., Kujala, H. & Leathwick, J.R. (2009) The Zonation framework and software for conservation prioritization. Spatial Conservation Prioritization (eds A. Moilanen, K.H. Wilson & H.P. Possingham), pp. 196–210. Oxford University Press.

Moilanen, A., Leathwick, J.R. & Quinn, J.M. (2011) Spatial prioritization of conservation management (eds A Moilanen, KA Wilson, and HP Possingham). Conservation Letters, 4, 383–393.

Moilanen, A., Possingham, H.P. & Polasky, S. (2009) A Mathematical Classification of Conseravation Prioritization Problems. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K. Wilson & H.P. Possingham), pp. 28–42. Oxford University Press, Oxford.

Moilanen, A., Possingham, H.P. & Wilson, K.A. (2009) Spatial Conservation Prioritization: Past, Present, and Future. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, H.P. Possingham & K.A. Wilson), p. 304. Oxford University Press, Oxford.

Moilanen, A., Pouzols, F.M., Meller, L., Veach, V., Arponen, A., Leppänen, J. & Kujala, H. (2014) Zonation Spatial Conservation Planning Methods and Software v. 4, User Manual. Helsinki.

Moilanen, A., Wilson, K.A. & Possingham, H.P. (2009) Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, Oxford, UK.

Moilanen, A. & Wintle, B.A. (2007) The Boundary-Quality Penalty: a Quantitative Method for Approximating Species Responses to Fragmentation in Reserve Selection. Conservation Biology, 21, 355–364.

Mäntymaa, E., Juutinen, A., Mönkkönen, M. & Svento, R. (2009) Participation and compensation claims in voluntary forest conservation: A case of privately owned forests in Finland. Forest Policy and Economics, 11, 498–507.

Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H. & Tikkanen, O.-P. (2014) Spatially dynamic forest management to sustain biodiversity and economic returns. Journal of environmental management, 134C, 80–89.

Mönkkönen, M., Reunanen, P., Kotiaho, J.S., Juutinen, A., Tikkanen, O.-P. & Kouki, J. (2011) Cost-effective strategies to conserve boreal forest biodiversity and long-term landscape-level maintenance of habitats. European Journal of Forest Research, 130, 717–727.

Mönkkönen, M., Ylisirniö, A.-L. & Hämäläinen, T. (2009) Ecological efficiency of voluntary conservation of boreal-forest biodiversity. Conservation Biology, 23, 339–347.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H. & Rouget, M. (2006) Integrating economic costs into conservation planning. Trends in Ecology and Evolution, 21, 681–687.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, Dr., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H. & Shaw, Mr. (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment, 7, 4–11.

Nicholson, E. & Ovaskainen, O. (2009) Conservation Prioritization Using Metapopulation Models. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K.A. Wilson & H.P. Possingham), p. 304. Oxford University Press, Oxford.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E. & Ovaskainen, O. (2013) Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests (ed P Thrall). Journal of Ecology, 101, 701–712.

Normile, D. (2010) U.N. Biodiversity Summit Yields Welcome and Unexpected Progress. Science, 330, 742–743.

Norros, V., Penttilä, R., Suominen, M. & Ovaskainen, O. (2012) Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos, 121, 961–974.

Opdam, P. (2010) Learning science from practice. Landscape Ecology, 25, 821–823.

Openshaw, S. (1984) The modifiable areal unit problem. Concepts and Techniques in Modern Geography, 38 Norwich.

Paloniemi, R. & Tikka, P.M. (2008) Ecological and social aspects of biodiversity conservation on private lands. Environmental Science & Policy, 11, 336–346.

Parviainen, J. & Frank, G. (2003) Protected forests in Europe approaches-harmonising the definitions for international comparison and forest policy making. Journal of Environmental Management, 67, 27–36.

Pascual-Hortal, L. & Saura, S. (2007) Impact of spatial scale on the identification of critical habitat patches for the maintenance of landscape connectivity. Landscape and Urban Planning, 83, 176–186.

Perera, A.H., Drew, C.A. & Johnson, C.J. (2012) Experts, Expert Knowledge, and Their Roles in Landscape Ecological Applications. Expert Knowledge and Its Application in Landscape Ecology (eds A.H. Perera, C.A. Drew & C.J. Johnson), p. 307. Springer, Dordrecht.

Pert, P.L., Lieske, S.N. & Hill, R. (2013) Participatory development of a new interactive tool for capturing social and ecological dynamism in conservation prioritization. Landscape and Urban Planning, 114, 80–91.

Pfeffer, J. & Sutton, R.I. (1999) Knowing "What" to Do Is Not Enough: Turning Knowlede Into Action. California management review, 42, 83–108.

Pierce, S.M., Cowling, R.M., Knight, A.T., Lombard, A.T., Rouget, M. & Wolf, T. (2005) Systematic conservation planning products for land-use planning: Interpretation for implementation. Biological Conservation, 125, 441–458.

Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S.C. & Pulliam, H.R. (2001) Making Smart Conservation Decisions. Research Priorities for Conservation Biology (eds G. Orians & M. Soulé), pp. 225–244. Washington D.C.

Possingham, H.P., Ball, I.R. & Andelman, S.J. (2000) Mathematical methods for identifying representative reserve networks. Quantitative methods for conservation biology (eds S. Ferson & M.A. Burgman), pp. 291–305. Springer-Verlag, New York.

Pouzols, F.M., Burgman, M.A. & Moilanen, A. (2012) Methods for allocation of habitat management, maintenance, restoration and offsetting, when conservation actions have uncertain consequences. Biological Conservation, 153, 41–50.

Pouzols, F.M. & Moilanen, A. (2013) RobOff: Software for analysis of alternative land-use options and conservation actions. Methods in Ecology and Evolution, 4, 426–432.

Prendergast, J.R., Quinn, R.M. & Lawton, J.H. (1999) The Gaps between Theory and Practice in Selecting Nature Reserves. Conservation Biology, 13, 484–492.

Pressey, R.L. & Bottrill, M.C. (2009) Approaches to landscape- and seascape-scale conservation planning: convergence, contrasts and challenges. Oryx, 43, 464.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. Trends in Ecology and Evolution, 22, 583–592.

Pressey, R.L., Mills, M., Weeks, R. & Day, J.C. (2013) The plan of the day: Managing the dynamic transition from regional conservation designs to local conservation actions. Biological Conservation, 166, 155–169.

Pressey, R.L., Watts, M.E., Barrett, T.W. & Ridges, M.J. (2009) The C-Plan Conservation Planning System: Origins, Applications and Possible Futures. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A. Moilanen, K. Wilson & H.P. Possingham), pp. 211–234. Oxford University Press.

Primmer, E. (2011) Analysis of institutional adaptation: integration of biodiversity conservation into forestry. Journal of Cleaner Production, 19, 1822–1832.

Primmer, E. & Kyllönen, S. (2006) Goals for public participation implied by sustainable development, and the preparatory process of the Finnish National Forest Programme. Forest Policy and Economics, 8, 838–853.

Primmer, E., Paloniemi, R., Similä, J. & Barton, D.N. (2013) Evolution in Finland's Forest Biodiversity Conservation Payments and the Institutional Constraints on Establishing New Policy. Society & Natural Resources, 26, 1137–1154.

Primmer, E., Paloniemi, R., Similä, J. & Tainio, A. (2014) Forest owner perceptions of institutions and voluntary contracting for biodiversity conservation: Not crowding out but staying out. Ecological Economics, 103, 1–10.

Proctor, S., McClean, C.J. & Hill, J.K. (2011) Protected areas of Borneo fail to protect forest landscapes with high habitat connectivity. Biodiversity and Conservation, 20, 2693–2704.

Pukkala, T. (2004) Dealing with Ecological Objectives in the Monsu Planning System. Silva Lusitana, 1–15.

Pullin, A.S., Knight, T.M., Stone, D.A. & Charman, K. (2004) Do conservation managers use scientific evidence to support their decision-making? Biological Conservation, 119, 245–252.

Python Development Team. (2014) Python Language Reference, Version 2.7. Python Software Foundation.

R Core Team. (2014) R: A Language and Environment for Statistical Computing, Version 3.1.0. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters, 8, 224–239.

Ram, K. (2013) Git can facilitate greater reproducibility and increased transparency in science. Source Code for Biology and Medicine, 8, 1–14.

Ranius, T. & Kindvall, O. (2006) Extinction risk of wood-living model species in forest landscapes as related to forest history and conservation strategy. Landscape Ecology, 21, 687–698.

Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. (2010) The 2010 Red List of Finnish Species. Helsinki.

Rayfield, B., Fortin, M.-J. & Fall, A. (2011) Connectivity for conservation: a framework to classify network measures. Ecology, 92, 847–858.

Rayfield, B., James, P.M.A., Fall, A. & Fortin, M.-J. (2007) Comparing static versus dynamic protected areas in the Québec boreal forest. Biological Conservation, 141, 438–449.

Rayfield, B., Moilanen, A. & Fortin, M.-J. (2009) Incorporating consumer-resource spatial interactions in reserve design. Ecological Modelling, 220, 725–733.

Richardson, E.A., Kaiser, M.J., Edwards-Jones, G. & Possingham, H.P. (2006) Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. Conservation Biology, 20, 1191–1202.

Rondinini, C., Wilson, K. a, Boitani, L., Grantham, H. & Possingham, H.P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. Ecology Letters, 9, 1136–1145.

Runge, M.C., Converse, S.J. & Lyons, J.E. (2011) Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. Biological Conservation, 144, 1214–1223.

Runnel, K., Rosenvald, R. & Lõhmus, A. (2013) The dying legacy of green-tree retention: Different habitat values for polypores and wood-inhabiting lichens. Biological Conservation, 159, 187–196.

Salminen, H. & Hynynen, J. (2001) Motti; a growth and yield simulation system. Proceedings of the Conference on Forest Modelling for Ecosystem Management, Forest Certification, and Sustainable Management, Vancouver, BC, Canada, August 12–17 (eds V. LeMay & P. Marshall), p. 488.

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S.J. (2006) Biodiversity conservation planning tools: Present status and Challenges for the future. Annual Review of Environment and Resources, 31, 123–159.

Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C. & Estes, J. (2001) Nature reserves: Do they capture the full range of America's biological diversity? Ecological Applications, 11, 999–1007.

Segerson, K. & Miceli, T.J. (1998) Voluntary Environmental Agreements: Good or Bad News for Environmental Protection? Journal of Environmental Economics and Management, 36, 109–130.

Selonen, V. & Hanski, I.K. (2004) Young flying squirrels (Pteromys volans) dispersing in fragmented forests. Behavioral Ecology, 15, 564–571.

Siitonen, J. (2001) Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. Ecological Bulletins, 49, 11–41.

Siitonen, J. (2012) Threatened saproxylic species. Biodiversity in dead wood (eds J.N. Stokland, J. Siitonen & B.G. Jonsson), pp. 356–379. Cambridge University Press, Cambridge.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management, 128, 211–225.

Siitonen, J., Penttilä, R. & Ihalainen, A. (2012) METSO-ohjelman uusien pysyvien ja määräaikaisten suojelualueiden ekologinen laatu Uudenmaan alueella. Metsätieteen aikakausikirja, 259–284.

Siitonen, P., Tanskanen, A. & Lehtinen, A. (2002) Method for Selection of Old-Forest Reserves. Conservation Biology, 16, 1398–1408.

Similä, J., Fredrikson, J., Primmer, E. & Horne, P. (2014) Biodiversity Protection in Private Forests: An Analysis of Compliance. Journal of Environmental Law, 26, 83–103.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L. & Huhta, E. (2006) Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests ? Ecological Indicators, 6, 686–700.

Speirs-Bridge, A., Fidler, F., McBride, M., Flander, L., Cumming, G. & Burgman, M.A. (2010) Reducing overconfidence in the interval judgments of experts. Risk analysis, 30, 512–23.

St. John, R. & Tóth, S.F. (2013) Spatially explicit forest harvest scheduling with difference equations. Annals of Operations Research, 1–23.

Stohlgren, T.J., Chong, G.W., Kalkhan, M.A. & Schell, L.D. (1997) Multiscale Sampling of Plant Diversity: Effects of Minimum Mapping Unit Size. Ecological Applications, 7, 1064–1074.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012) Introduction. Biodiversity in dead wood (eds J.N. Stokland, J. Siitonen & B.G. Jonsson), pp. 1–9. Cambridge University Press, Cambridge.

Stoms, D.M. (1992) Effects of habitat map generalization in biodiversity assessment. Photogrammetric Engineering and Remote Sensing, 58, 1587–1591.

Stoms, D.M. (1994) Scale Dependence of Species Richness Maps. The Professional Geographer, 46, 346–358.

Store, R. & Jokimäki, J. (2003) A GIS-based multi-scale approach to habitat suitability modeling. Ecological Modelling, 169, 1–15.

Store, R. & Kangas, J. (2001) Integrating spatial multi-criteria evaluation and expert knowledge for GIS-based habitat suitability modelling. Landscape and Urban Planning, 55, 79–93.

Thomson, J., Moilanen, A., Vesk, P.A., Bennett, A., Nally, R. Mac & MacNally, R.M. (2009) Where and when to revegetate: a quantitative method for scheduling landscape reconstruction. Ecological applications, 19, 817–828.

Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. (2011) Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests. Biological Conservation, 144, 2061–2067.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. & Mönkkönen, M. (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. Scandinavian Journal of Forest Research, 25, 309–324.

Tomppo, E.O. (1990) Satellite image-based national forest inventory of Finland. The Photogrammetric Journal of Finland, 12, 115–120.

Tomppo, E.O. (2006a) The Finnish National Forest Inventory. Forest inventory: Methodology and applications, Managing F (eds A. Kangas & M. Maltamo), pp. 179–194. Springer, Dordrecht.

Tomppo, E.O. (2006b) The Finnish multi-source National Forest Inventory-small area estimation and map production. Forest inventory: Methodology and Applications (eds A. Kangas & M. Maltamo), pp. 195–224. Springer, Dordrecht.

Tomppo, E.O., Haakana, M., Kaitila, M. & Peräsaari, J. (2008) Multi-Source National Forest Inventory – Methods and Applications. Springer, Dordrecht.

Tuominen, S., Balazs, A., Korhonen, K.T. & Muinonen, E. (2014) NFI plots as complementary reference data in forest inventory based on airborne laser scanning and aerial photography in Finland. Silva Fennica, 48, 1–20.

Tversky, B. (2000) Some ways that maps and diagrams communicate. Spatial Cognition II - Integrating Abstract Theories, Empirical Studies, Formal Methods, and Practical Applications (eds C. Freksa, C. Habel, W. Brauer & K.F. Wender), pp. 72–79. Springer, Dordrecht.

Uhlir, P.F. & Schröder, P. (2007) Open data for global science. Data Science Journal, 6, 36–53.

Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B. & Pressey, R.L. (2004) Sensitivity of Systematic Reserve Selection to Decisions about Scale, Biological Data, and Targets: Case Study from Southern British Columbia. Conservation Biology, 18, 655–666.

Watts, M.E., Ball, I.R., Stewart, R.S., Klein, C.J., Wilson, K.A., Steinback, C., Lourival, R., Kircher, L. & Possingham, H.P. (2009) Marxan with Zones: Software for optimal conservation based land- and sea-use zoning. Environmental Modelling & Software, 24, 1–9.

Vierikko, K., Vehkamäki, S., Niemelä, J., Pellikka, J. & Lindén, H. (2008) Meeting the ecological, social and economic needs of sustainable forest management at a regional scale. Scandinavian Journal of Forest Research, 23, 431–444.

Williams, P.H., Faith, D., Manne, L., Sechrest, W. & Preston, C. (2005) Complementarity analysis: Mapping the performance of surrogates for biodiversity. Biological Conservation, 8, 253–264.

Williams, J.C., Revelle, C.S. & Levin, S.A. (2004) Using Mathematical Optimization Models to Design Nature Reserves Author. Frontiers in Ecology and the Environment, 2, 98–105.

Williams, J.C., Revelle, C.S. & Levin, S.A. (2005) Spatial attributes and reserve design models: A review. Environmental Modeling & Assessment, 10, 163–181.

Wilson, K.A., Cabeza, M. & Klein, C.J. (2009) Fundamental Concepts of Spatial Conservation Prioritization. Spatial Conservation Prioritization: Quantitative Methods & Computational Tools (eds A.J. Moilanen, K.A. Wilson & H.P. Possingham), pp. 16–27. Oxford University Press, Oxford.

Wilson, K. a, Carwardine, J. & Possingham, H.P. (2009) Setting conservation priorities. Annals of the New York Academy of Sciences, 1162, 237–264.

Wilson, K., Pressey, R.L., Newton, A.C., Burgman, M., Possingham, H. & Weston, C. (2005) Measuring and incorporating vulnerability into conservation planning. Environmental Management, 35, 527–543.

Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S.J., Looker, M., Rondinini, C., Kareiva, P.M., Shaw, M.R. & Possingham, H.P. (2007) Conserving Biodiversity Efficiently: What to Do, Where, and When (ed GM Mace). PLoS Biology, 5, 12.

Virkkala, R., Korhonen, K.T., Haapanen, R. & Aapala, K. (2000) Protected Forests and Mires in Forest and Mire Vegetation Zones in Finland based on the 8th National Forest Inventory. Finnish Envronment, 395, 1–49.

Virkkala, R. & Rajasärkkä, A. (2006) Uneven regional distribution of protected areas in Finland : Consequences for boreal forest bird populations. Biological Conservation, 4.

Virolainen, K.M., Nättinen, K., Suhonen, J. & Kuitunen, M. (2001) Selecting herb-rich forest networks to protect different measures of biodiversity. Ecological Applications, 11, 411–420.

Wolkovich, E.M., Regetz, J. & O'Connor, M.I. (2012) Advances in global change research require open science by individual researchers. Global Change Biology, 18, 2102–2110.

Wätzold, F. & Schwerdtner, K. (2005) Why be wasteful when preserving a valuable resource? A review article on the cost-effectiveness of European biodiversity conservation policy. Biological Conservation, 123, 327–338.